

## COMPARATIVE ANATOMY AND RELATIONSHIPS OF COLUMELLIACEAE

WILLIAM L. STERN, GEORGE K. BRIZICKY,<sup>1</sup>  
AND RICHARD H. EYDE

Género dedicado á Junio Moderato Columela, antiguo español, colocado por Linneo entre los padres de la Botánica, y que escribió elegantemente en prosa y verso de *Labranza y cultivo de Jardines* — Ruiz and Pavón 1794.

IN 1961, Brizicky summarized information on the Andean genus *Columellia* and presented a taxonomic synopsis of this puzzling group of plants. The genus was described in 1794 by Ruiz and Pavón and David Don established Columelliaceae in 1828. Eleven species have at one time or another been ascribed to the genus and through his critical examination of all available herbarium specimens, Brizicky reduced this number to four more or less well-defined species. Evaluations of the taxonomic position of *Columellia* and Columelliaceae have been set forth from the time of A. L. de Jussieu and Ruiz and Pavón, but even the latest authors have been unable to fix the relationships of these plants conclusively. "With its peculiar combination of opposite, exstipulate leaves; bisexual, epigynous flowers; somewhat irregular, sympetalous corollas; two stamens with plicate and contorted anthers resembling those of some Cucurbitaceae; two-carpellate, imperfectly two-locular ovaries; and imperfectly four-locular capsular fruits, *Columellia* is indeed a unique genus" (Brizicky 1961).

Although several positions have been proposed for *Columellia* and for Columelliaceae, taxonomists agree that a plausible understanding of the relationships of these plants requires comprehensive studies to clarify disputed points and to complete our knowledge of their anatomy. It was with this in mind that the present authors have examined the anatomy of the flower and fruit, node, leaf, and secondary xylem.

### Taxonomic position of *Columellia*

A. L. de Jussieu (1801) considered *Columellia* as a genus of Oleaceae "hoc Genus ad Jasminearum ordinem pertinere." Kunth (1818) placed the genus in Scrophularinae, but noted, "An Gesnereis affinior?" At first Reichenbach (1828) included the genus in Gesneriaceae ("Gesnereae" as a tribe of Bignoniaceae) but later (1837) he transferred it to Oleaceae

<sup>1</sup> George K. Brizicky died June 15, 1968 in Cambridge, Massachusetts, during the final stages of the preparation of this manuscript. It is to his memory that the surviving authors respectfully dedicate this paper.

("Jasmineae"). Bartling (1830) retained *Columellia* in Scrophulariaceae among "Genera incertae sedis." Sprengel (1830) supposed the affinity of the genus to be with Gesneriaceae. In 1839, Endlicher placed *Columellia* near Ebenaceae among "Genera Dubiae Affinitatis"; later (1841), he included it in his classis (order) Petalanthae (Primulaceae, Myrsinaceae, Sapotaceae, Ebenaceae, and Styracaceae) as a genus "Petalanthis affinis." Schnizlein (1843–1870) recommended an affinity with Saxifragaceae-Escallonioideae ("Escallonieen"), and particularly with the genera *Argophyllum* J. R. & G. Forst., *Brexia* Nor. ex Thou., and *Roussea* Smith. J. D. Hooker (1873, 1875) suggested referring the genus to Loganiaceae. Baillon (1888) included *Columellia* in Gesneriaceae as a representative of the monogeneric series Columellieae (between series Gesnereae and series Cyrtandreae). Hallier at first (1901) placed *Columellia* in Rubiaceae as an anomalous genus and later (1903) included it in Scrophulariaceae as questionably related to *Veronica* sect. *HEBE* Benth. of the tribe Leucophylleae. Finally (1908, 1910) he transferred it to Saxifragaceae-Philadelphaeae. Herzog (1915) also regarded *Columellia* as a genus of Saxifragaceae.

#### Taxonomic position of Columelliaceae

David Don (1828), who founded the family Columelliaceae, considered it allied to Oleaceae ("Oleinae" and "Jasmineae") as well as to Styracaceae and Ebenaceae. Apparently following the suggestions of his brother, George Don (1838) showed Columelliaceae ("Columellieae") to contain three genera: *Columellia*, *Menodora* Humb. & Bonpl., and *Bolivaria* Cham. & Schlechtd. (= *Menodora* Humb. & Bonpl.). He placed the family between Oleinae and Jasmineaceae. Grisebach (1839) presumed a close relationship with Gentianaceae. Meisner (1836–1843) favored the affinity of Columelliaceae with Oleaceae. De Candolle (1839) assumed a close relationship with Gesneriaceae. Adrien de Jussieu (1848) placed Columelliaceae in Rubiales between Caprifoliaceae and Valerianaceae. Lindley (1835) put Columelliaceae in his alliance (order) Cinchonales (Rubiales) between Vacciniaceae and Cinchonaceae (Rubiaceae) with which families and Onagraceae he thought it related. He also presumed an affinity of Columelliaceae with Caprifoliaceae. Agardh (1858) suggested a close affinity of the family with Lythraceae ("Lawsoniae"). Basing his conclusions on the contorted anthers in both Columelliaceae and Cucurbitaceae, Clarke (1858) asserted that, ". . . if the nearest affinity of this family [Columelliaceae] is not with Cucurbitaceae, yet there is no other to which it more closely approaches. . . ." Following de Candolle, Bentham and Hooker (1876), and several of the more recent taxonomists — Fritsch 1894, Engler 1892 (unchanged in Melchior's 1964 edition of Engler's "Syllabus der Pflanzenfamilien"), Schlechter 1920, Wettstein 1935, and Pulle 1952 — placed Columelliaceae near Gesneriaceae. Fritsch emphasized the similarity with *Bellonia* L. (Gesneriaceae). Nevertheless, Wettstein stressed the continuing uncertainty of the systematic position of Columelliaceae. Warburg (1922) placed Columelliaceae near Gesneriaceae also; however, he noted: "Am natürlichsten dürfte die

Stellung bei den Rubiaceen sein." In 1959, Takhtajan allied Columelliaceae closely to Gesneriaceae, particularly with the genus *Ramonda* Rich. Here, and in his 1966 work, he stated that Columelliaceae is a derivative of Gesneriaceae. Hutchinson (1959) placed Columelliaceae in Personales with the families Scrophulariaceae, Acanthaceae, Gesneriaceae, Orobanchaceae, and Lentibulariaceae. Airy Shaw (in Willis 1966) stated: "Despite the sympetaly, slight zygomorphy and curious anthers [in Columelliaceae], probably related to *Escalloniac.* and *Hydrangeac.*; perhaps also to *Loganiac.*" In his recent conservative treatment of Saxifragaceae, Thorne (1968) treated Columelliaceae as a subfamily adjacent to Escallonioideae and Montinioideae. Columelliaceae is placed in Rosales by Cronquist (1968) near the Pittosporaceae and Grossulariaceae.

Anatomists have examined the microscopic structure of Columelliaceae in an attempt to establish its affinities with more certainty. Solereder (1899) was able to study the structure of *Columellia oblonga* Ruiz & Pavón ssp. *serrata* (Rusby) Brizicky (= *C. serrata* Rusby) and concluded that the occurrence of scalariform perforation plates and fibrous elements with conspicuous bordered pits in the secondary xylem precluded any close affinity with Gesneriaceae. Rather, he thought, Columelliaceae showed anatomical similarities to Saxifragaceae. Van Tieghem (1903), having several species of *Columellia* at his disposal, confirmed Solereder's anatomical observations, thus establishing the homogeneity of secondary xylem structure throughout the genus. However, van Tieghem believed Columelliaceae to be best placed in his alliance Rubiales near Rubiaceae. Metcalfe and Chalk (1950), having no further material at their disposal, repeated Solereder's findings. Erdtman (1952) stated that pollen morphology of Columelliaceae does not give any positive indications of the affinity of the family. He does remark, however, that "The following families have been mentioned as possibly related [to Columelliaceae]: Ebenaceae, Ericaceae, Gesneriaceae (the grains of *Bellonia* [Gesneriaceae] are not similar to those of *Columellia*!). . . ."

*Columellia*, or Columelliaceae, has been considered related to families of both Sympetalae and Choripetalae, to families with superior ovaries and to others with inferior ovaries. Some proposed relatives have stipules and others are exstipulate; some proposed relatives have opposite leaves and others have alternate leaves; some proposed related families are largely herbaceous and others are mostly woody. Among the taxa suggested as relatives, the following seem to predominate: The first proposals indicated Oleaceae; later the Ericaceae-Vaccinioideae and Rubiaceae were recommended; Scrophulariaceae appeared a few times in the literature during the early 19th century; but Gesneriaceae seemed most strongly defended in the late 19th and early 20th centuries. Although alliance with Saxifragaceae was suggested in the mid-19th century, it was not until the early 20th century and later that the proposal seemed to gain strength. Several other families have been proposed, though not as often as the foregoing: Ebenaceae, Styracaceae, Gentianaceae, Loganiaceae, Capri-

foliaceae, and Onagraceae. Today, both the gesneriaceous and saxifragaceous hypotheses of relationship seem to have equal standing among plant taxonomists, although the most recent treatments favor alignment with saxifragaceous taxa. It is clear, though, that the variety of families proposed as relatives of *Columellia* (Columelliaceae) could not be much more diverse.

#### MATERIALS AND METHODS

In drawing comparisons between Columelliaceae and other families, it has been necessary for convenience and clarity to accept certain taxonomic delineations and judgements. This is especially important in referring to the Saxifragaceae which has been treated in different ways by different authors. Engler's (1928) treatment is the most detailed to date and his concept of the family is very broad. He divides Saxifragaceae into several subfamilies, namely, Penthoroideae, Saxifragoideae, Lepuropetaloidae, Parnassioideae, Tetracarpaeoideae, Pterostemonoideae, Iteoidae, Brexioideae, Kirengeshomoideae, Kanioideae, Baueroideae, Hydrangeoideae, Escallonioideae, Montinioideae, and Phyllonomoideae. Thorne's (1968) outline is very reminiscent of Engler's treatment. In our paper, when "Saxifragaceae, *sensu lato*," is employed, it is used in this broad Englerian sense.

Other taxonomists have chosen to disassemble the Englerian conglomerate into several smaller families; hence, Hutchinson (1967) treated Engler's subfamily Escallonioideae as the family Escalloniaceae and his subfamily Hydrangeoideae as the family Hydrangeaceae. Engler's tribe Philadelphae of Hydrangeoideae is considered as Philadelphaceae by Hutchinson. The genus *Ribes* L. is part of the subfamily Saxifragoideae in Engler but Hutchinson treated it as the basis of the monogeneric family, Grossulariaceae. Cronquist (1968), similarly, has dissected Engler's Saxifragaceae. Because our comparisons among the vegetative parts of plants depend heavily on the information in Metcalfe and Chalk (1950), we have used their taxonomic designations for the Englerian subfamilies. The concept of Saxifragaceae employed by these two plant anatomists is wholly herbaceous, and the woody taxa in Engler's Saxifragaceae are relegated to other families, e.g., Escalloniaceae, Grossulariaceae, and Hydrangeaceae (including Hutchinson's Philadelphaceae). "Saxifragaceae, *sensu stricto*," as we have used it, refers to a strictly herbaceous family conforming to the sense of Metcalfe and Chalk.

Terminology used in the descriptions of xylem anatomy follows that prescribed by the Committee on Nomenclature of the International Association of Wood Anatomists (1957). Other terminology used in descriptions of anatomical structures is that in current use and deviations from common usage are explained where they occur.

TABLE 1 contains a detailed listing of specimens employed in the study of the vegetative anatomy of *Columellia*; materials used for comparative

floral anatomy are cited in the text. Fluid-preserved material of about 30 flowers of *C. oblonga* ssp. *oblonga* was available from one of Továr's collections (4033, USM). All study specimens of wood, stems, leaves, and flowers (except for comparative floral material of *Escallonia* and *Carpodetus*), are supported by herbarium vouchers and their place of deposit is noted in TABLE 1 or in the text.

Methods of preparing specimens for study followed standard laboratory techniques. Woods were boiled in water to hydrate and stored in 70 percent ethanol prior to microtoming. Transverse, radial, and tangential sections of wood were stained with Heidenhain's iron-alum haematoxylin and counter-stained with safranin. Macerations of wood were prepared using Jeffrey's fluid. Clearing of leaves was carried out using Arnott's (1959) method involving 5 percent NaOH followed by a saturated aqueous solution of chloral hydrate. After washing in water, leaves were stained in aqueous safranin to accentuate vascular detail, dehydrated, and mounted on glass slides in Canada balsam. Transverse and paradermal sections of leaves were also prepared after embedding in paraffin. These were stained in Heidenhain's iron-alum haematoxylin and safranin. Nodal and petiolar anatomy were studied from hand-cut sections treated with phloroglucinol and concentrated HCl to differentiate the lignified tissues. Observations of floral anatomy were performed from serial microtome sections (transverse and longitudinal), cleared thick sections, and cleared whole flowers of *Columellia oblonga* ssp. *oblonga*. These preparations were made using familiar microtechnical methods from flowers fixed in formalin-acetic acid-alcohol.

## ANATOMY

### The flower

Transverse sections through the base of the *Columellia* gynoecium show two locules separated by a thick septum (FIG. 1, d, d<sup>1</sup>). In successively more distal sections the placentas appear first as single lobes on each side of the septum (FIG. 1, e; FIG. 3), then as deeply two-lobed structures bearing many unitegmic ovules (FIG. 1, f). In still more distal sections there is an opening between the locules (FIG. 1, g, h), but the uppermost level of the ovary may again be divided by a complete septum (FIG. 2) through which the stylar canal enters the ovarian cavity.

If the stylar canal is followed distally its appearance in transverse section changes from that of a single cavity to that of a pair of tracts filled with pollen-transmitting tissue (FIG. 1, j, k). The pollen-transmitting tracts expand greatly below the two-lobed stigmatic surface, producing the unusual transectional effect shown in FIG. 4. The outer layers of gynoecial tissue, from the stylar base to the corolla, constitute a nectary of small cells with densely staining cytoplasm (FIG. 2).

Flowers of *Columellia* are devoid of unusual histologic features that can be used as taxonomic markers. The hypanthium, like the foliage, is

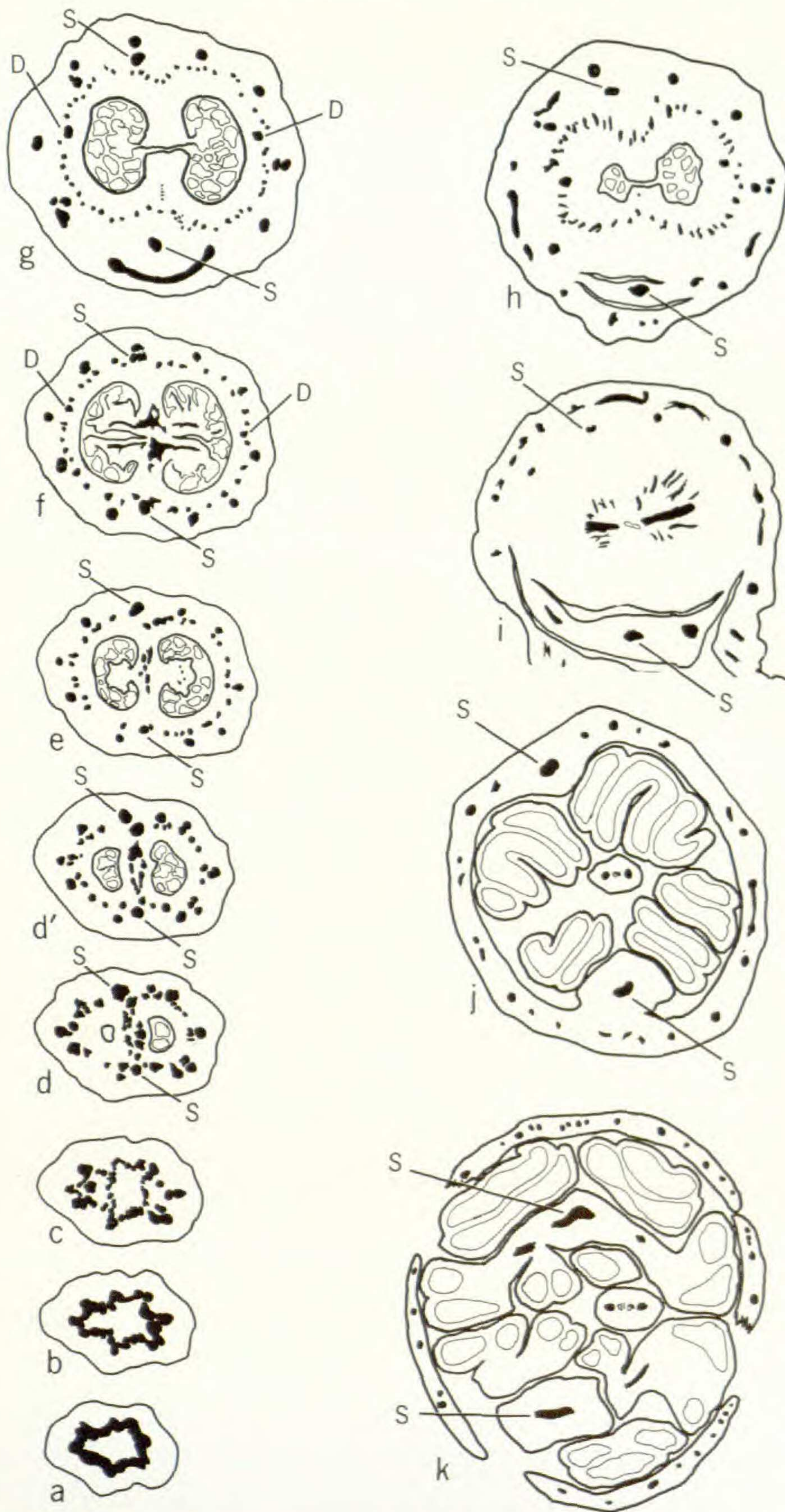
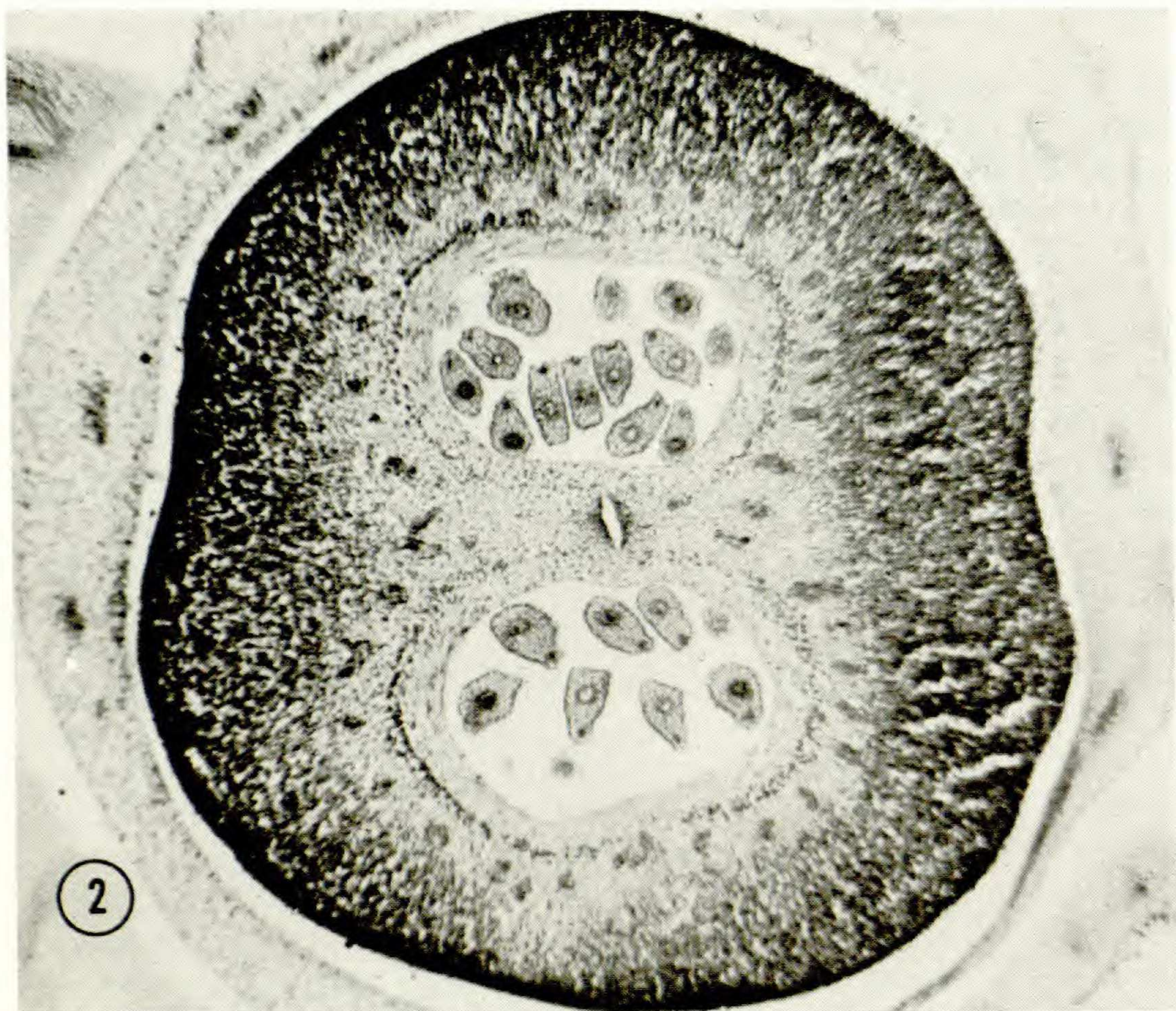


FIG. 1. *Columellia oblonga*, flower. Camera lucida drawings of selected transverse sections, arranged sequentially from pedicel (a) to upper part of flower (k). D, dorsal carpal bundles; S, stamen supply.



FIGS. 2 and 3. *Columellia oblonga*, flowers in transverse section. FIG. 2. Upper (free) part of gynoecium, showing nectary and upper ovarian septum,  $\times 30$ . FIG. 3. Lower part of flower showing basal septum, arrangement of vascular bundles (cf. FIG. 1,e); arrows indicate bundles supplying the 2 stamens,  $\times 60$ .

covered with simple, appressed trichomes. Floral tissues contain no conspicuous tannin cells or sclereids and no crystal inclusions except for a few scattered druses. The anthers dehisce with the aid of the familiar subepidermal banded layer (FIGS. 6, 7); moreover, the sporogenous portions, in spite of their peculiar external form, resemble in section the corresponding parts of ordinary four-locular anthers. The anther sacs, at least the young ones, are minutely glandular-hairy at the margins, the glandular trichomes being more or less club-shaped. The gynoecium contains a well-marked endocarp tissue, four to six cells deep on the dorsal side of the locule, gradually decreasing in thickness in the vicinity of the septum and the placentas. Cell walls of the endocarp are neither lignified nor greatly thickened in newly opened flowers, and there is no anatomical indication of a dehiscence line at this stage.

Floral vascular bundles, many of them amphicribal, diverge from a continuous cylinder in the pedicel (FIG. 1, a, b). Well below the base of the locules, the cylinder expands into the pattern shown in FIG. 1, c, with an inner portion of the vascular tissue directed to the septum and the placentas and an outer portion directed to other parts of the flower. A few sections above this level, and still below the locules, the outer portion separates into two series of traces, a gynoecial series and a series supplying perianth and stamens. With additional branching at even higher levels (FIG. 1, d, d<sup>1</sup>, e), the gynoecial series contains as many as 20 bundles per carpel, and the other series (now outermost) contains about a dozen perianth traces plus two stamen traces. A stamen trace can be united for part of its length with the basal extension of a sepal midvein or it can be completely free of other bundles to the base of the flower. In either case, the position of the stamen traces is the same; they occupy roughly the same radius as the septum. The perianth traces, if followed distally, become the major veins of sepals and corolla lobes. As in many other kinds of flowers, there are lateral connections between these strands at the level where the calyx and corolla become free of the ovary wall, and minor strands diverge from the major ones within the perianth members. The vascular tissue of the stamen broadens within the filament (FIG. 1, k) and terminates in the connective with a great many short branches.

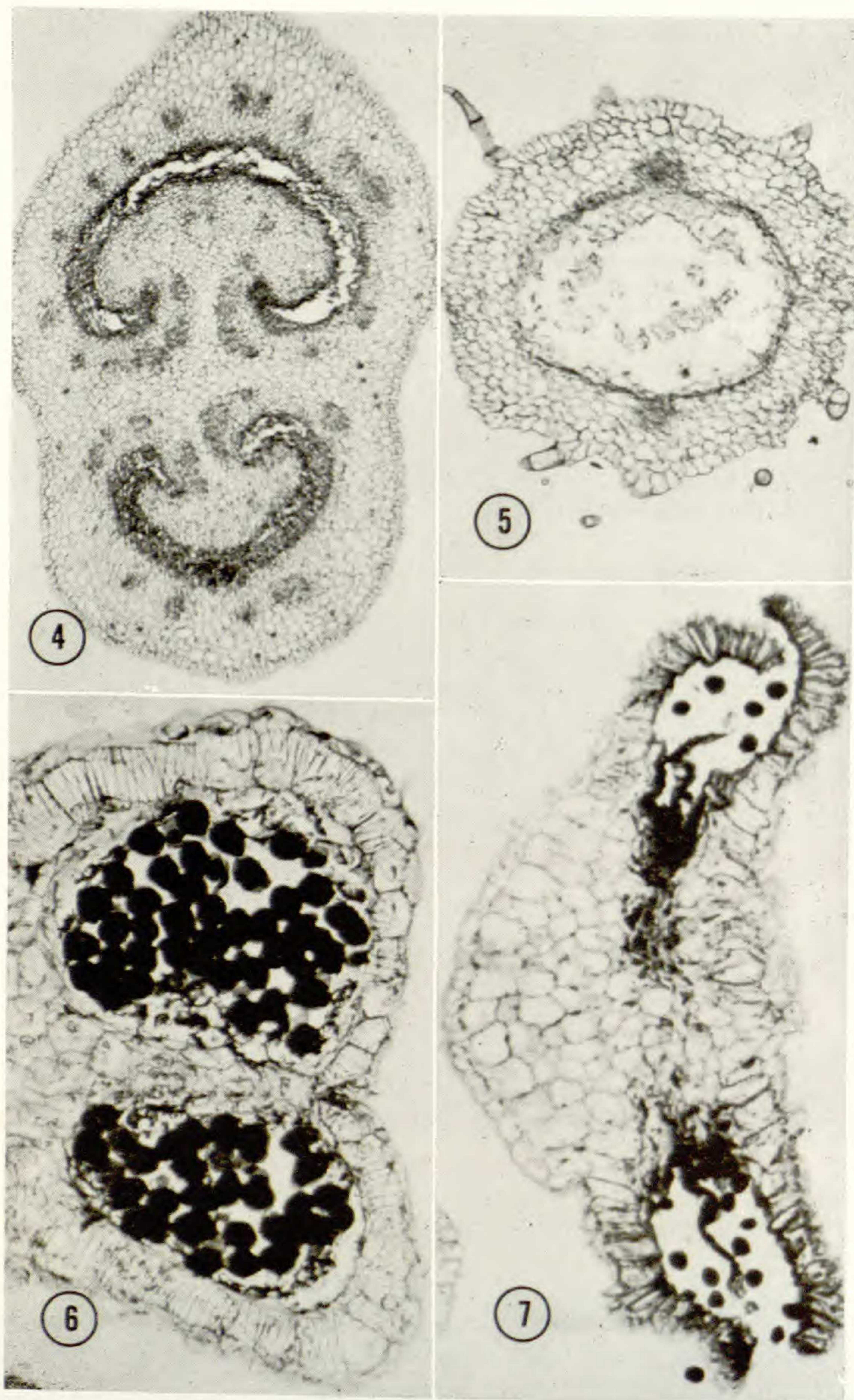
The vascular supply to the placentas rises through the septum in a massive and irregular column or plexus (FIG. 1, c-f). Branches to the ovules diverge from the plexus all through the placental region, but this portion of the vascular system does not continue above the placentas. The many outer gynoecial bundles, however, extend all the way to the base of the style (FIG. 1, g-i). Although the dorsal bundle is not easily distinguishable in sections through the lower half of the ovary, it is conspicuous in higher sections because of its proximity to the locule (FIG. 1, g, h). The dorsal bundle can be followed into the style, which it enters as a single well-defined strand. About a third of the way up the style, it divides into two or more strands, which subdivide further into many



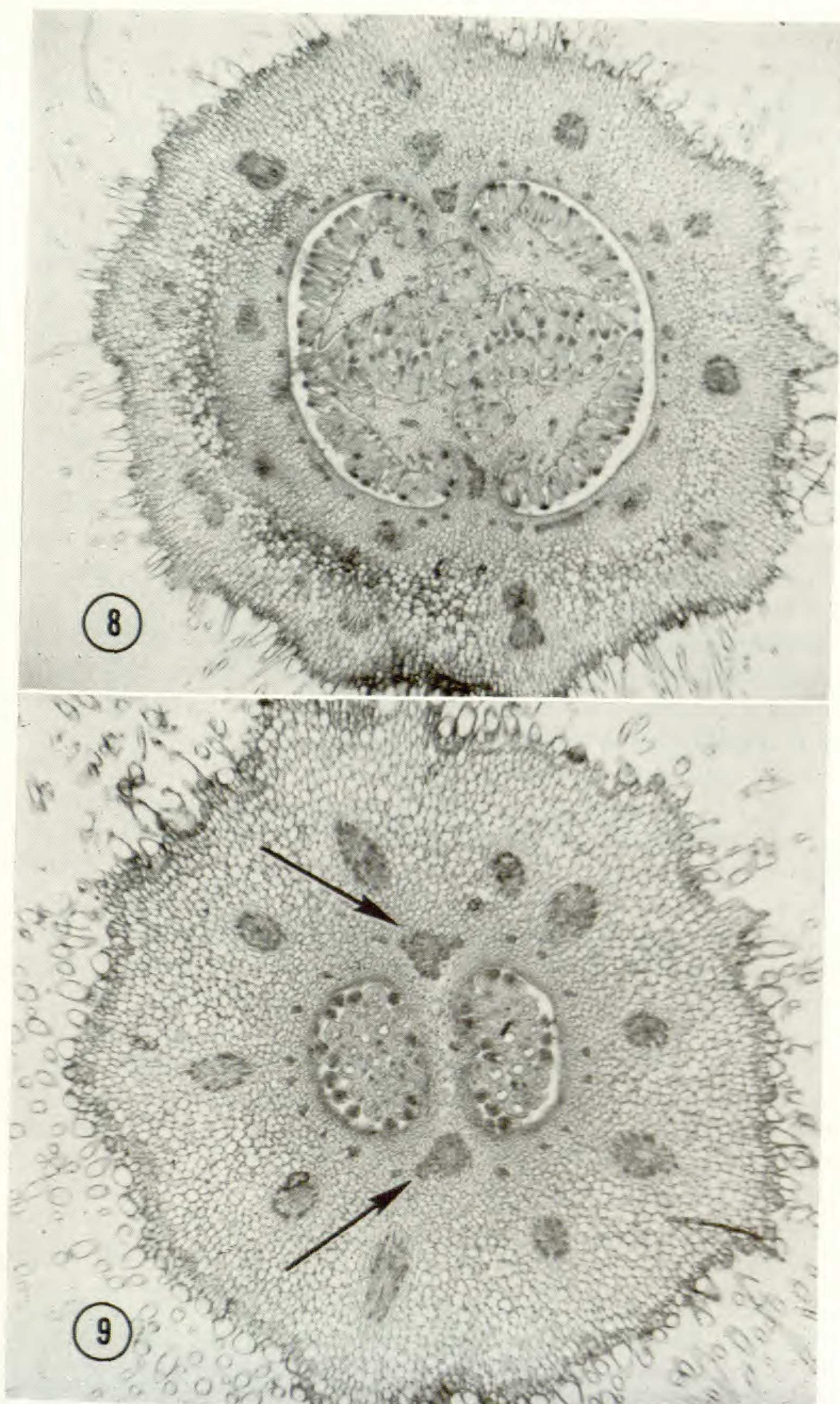
TABLE 1.  
Specimens of *Columellia* Examined

SPECIES	COLLECTOR	ORIGIN	VOUCHER	PARTS STUDIED *
<i>lucida</i> Danguy & Chermezon	André K-1444	Ecuador	F, GH	t
	André 4500	Ecuador	F, GH, NY	t
	Friedberg 240	Peru	US	l
	Mutis 2784	Colombia, <i>sine loco</i>	US	l
<i>oblonga</i> Ruiz & Pavón ssp. <i>oblonga</i>	Wurdack 1732	Peru	US	USw 32548, l
	Továr 4033	Peru	USM	USw, 36964, l, f
	Továr 3785	Peru	US	l
	Ruiz & Pavón 1/52	Peru	F	t
	Weberbauer 5584	Peru	F, GH, US	t, l
	Weberbauer 7791	Peru	A, F, MO, US	t, l
	Camp E-4461	Ecuador	GH, NY, Y, US	l
	Vargas 7408	Peru	US	l
	Cook & Gilbert 850	Peru	US	l
	Cook & Gilbert 1749	Peru	US	l
<i>oblonga</i> Ruiz & Pavón ssp. <i>sericea</i> (H.B.K.) Brizicky	Hitchcock 20846	Ecuador	GH, NY, US	l
	Rimbach 30	Ecuador	F, GH, Y	Yw 19496
	Rimbach 122	Ecuador	A, F, Y, US	Yw 22824, l
<i>oblonga</i> Ruiz & Pavón ssp. <i>serrata</i> (Rusby) Brizicky	Drew E-113	Ecuador	US	l
	Jameson <i>s.n.</i>	Ecuador	US 534794	l
	Jameson <i>s.n.</i>	Ecuador	US 534793	l
	Mille 44	Ecuador	A, GH, NY, US	l
	Mille 409	Ecuador	US	l
	Ownbey 2618	Ecuador	US	l
	Dodson & Thien 1067	Ecuador	US	l
	Asplund 7152	Ecuador	US	l
	Asplund 8003	Ecuador	US	l
	Wiggins 10351	Ecuador	US, DS	l
	Lehmann 4685	Ecuador	F, US	l
	Fosberg 21175	Colombia	US	l
	<i>oblonga</i> Ruiz & Pavón ssp. <i>serrata</i> (Rusby) Brizicky	Bang 1172	Bolivia	US
<i>obovata</i> Ruiz & Pavón	Weberbauer 5482	Peru	F, GH, US	t, l
	Herrera 3451	Peru	F	t
	Velardo Nuñez 3309	Peru	US	t, l
	Továr 1266	Peru	US	l
	Dombey <i>s.n.</i>	Peru	US 1706475	l
	Dombey <i>s.n.</i>	Peru	US 1706480	l
	Vargas 7693	Peru	MO, US	l

\*l = leaf, w = wood, t = twig, f = flower; abbreviations of institutional wood collections follow Stern (1967) and Stern and Chambers (1960).



FIGS. 4-7. FIG. 4. *Columellia oblonga*, transverse section through upper part of style,  $\times 55$ . FIG. 5. *Kohleria elegans* (Gesneriaceae), transverse section through upper part of style,  $\times 66$ . FIGS. 6 and 7. *C. oblonga*, transverse sections of anthers before and after dehiscence. FIG. 6,  $\times 125$ . FIG. 7,  $\times 95$ .



FIGS. 8 and 9. *Kohleria elegans* (Gesneriaceae), transverse sections through lower part of flower. FIG. 8. Placental region,  $\times 25$ . FIG. 9. Another flower, sectioned below placenta to show basal septum and ventral bundles (arrows),  $\times 34$ .

strands just below the stigma. The remaining bundles of the gynoecium wall converge upon the dorsal at the base of the style (FIG. 1, i); however, they do not appear to merge with the dorsal, because it enters the style with its cross-sectional shape and dimensions unchanged.

#### The leaf and the node

Hairs on leaves of *Columellia* are thick walled and simple, tapering to the obtuse tip and slightly swollen or bulbous at the base (FIGS. 10, 11). Trichomes emanate from the center of saucer-shaped depressions in the lower epidermis. These are formed from several radially oriented cells each of which is thicker toward the periphery of the depression and thinner toward the center where the hair arises (FIGS. 10, 11).

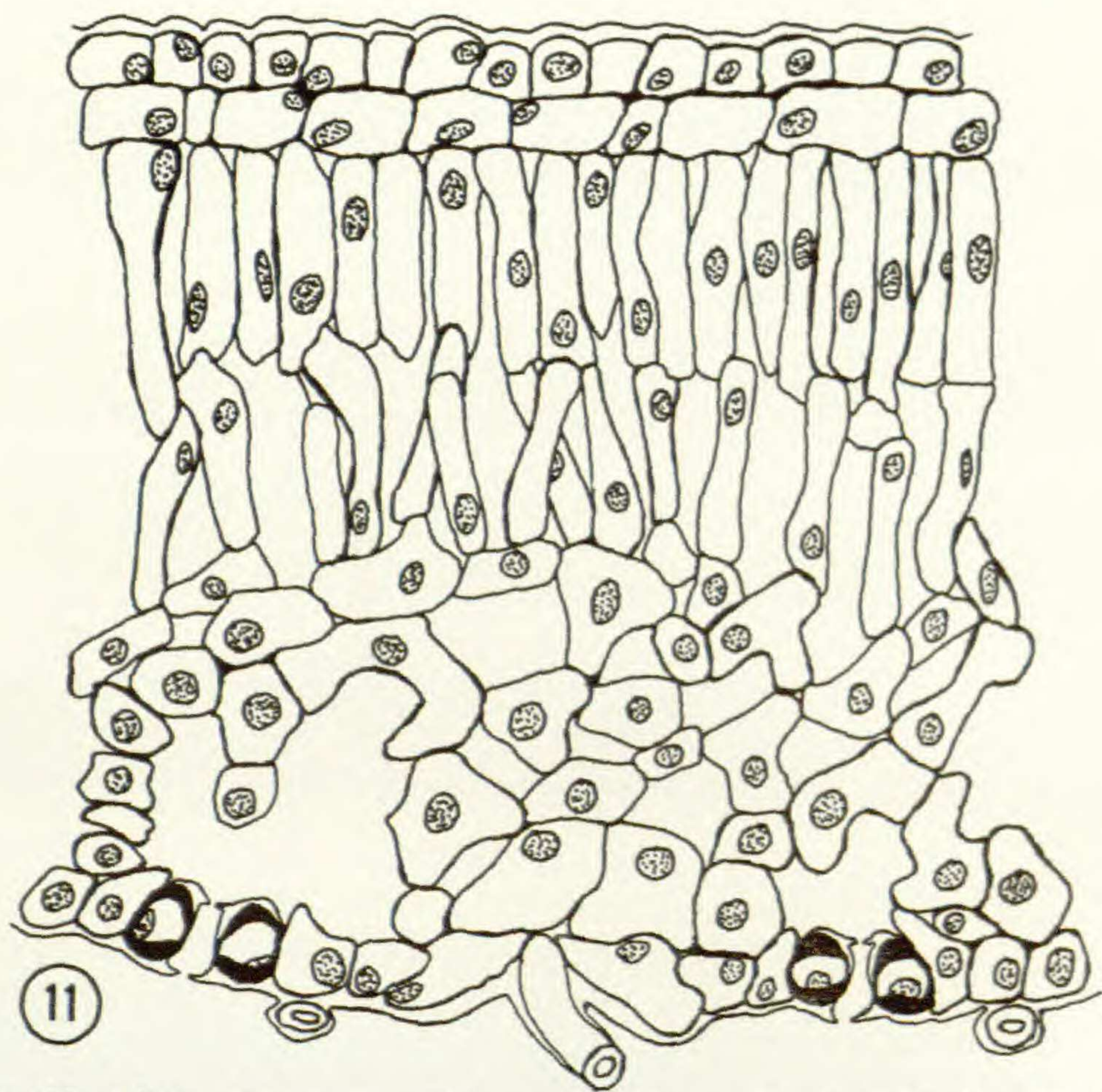
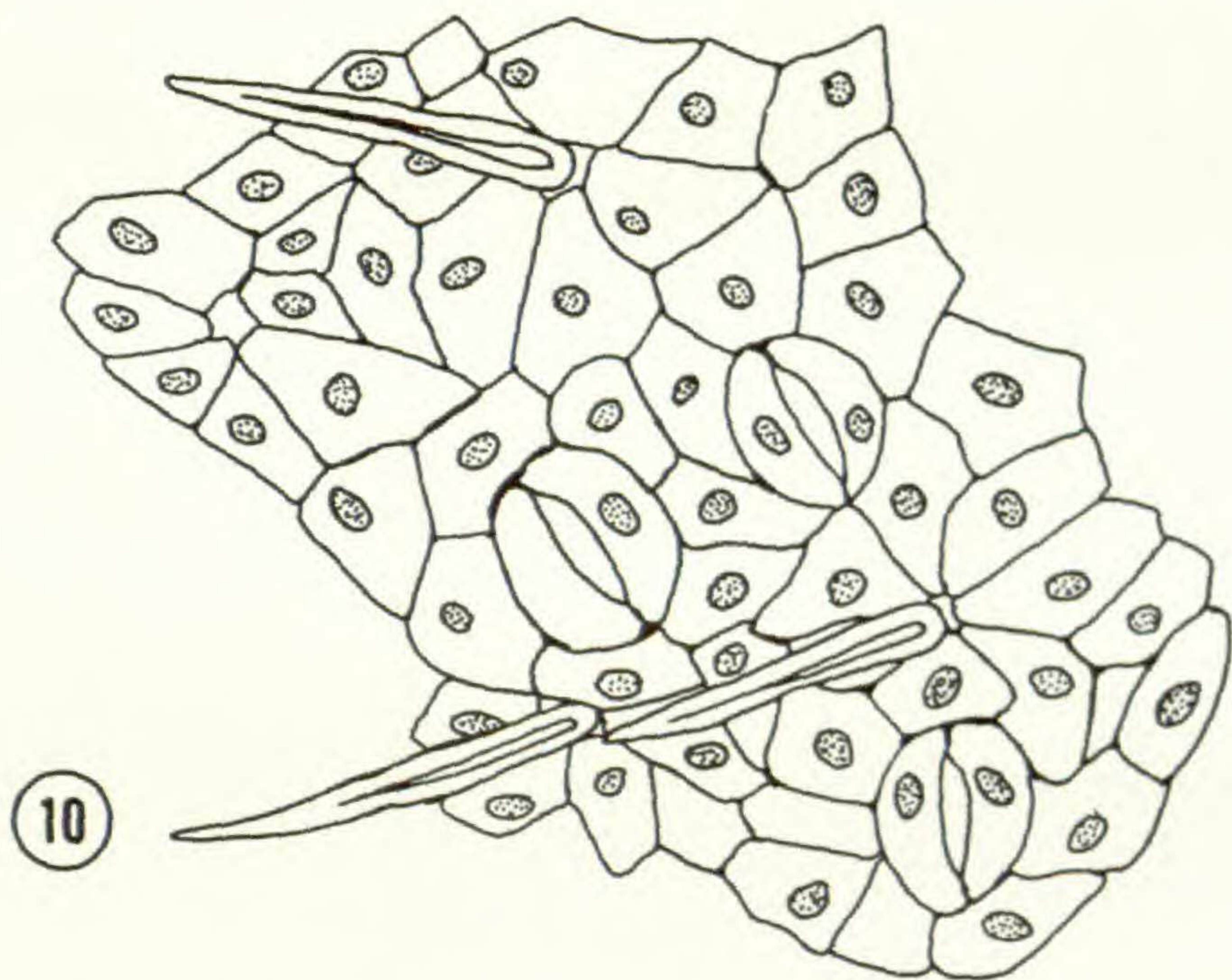
The cuticle is thick and covers upper and lower epidermis. It is especially pronounced toward leaf margins and in the trichome-base depressions of the lower epidermis. It also covers all portions of hairs. The cuticle is strongly modified in the stomatal region; it covers the exposed surfaces of guard cells and it over-arches both the outer portion of the aperture producing a front cavity and the inner portion producing a back cavity (FIGS. 11, 12).

Stomata are restricted to the lower epidermis. The stomatal apparatus<sup>2</sup> is anomocytic (*sensu* Metcalfe and Chalk, 1950), i.e., the guard cells are surrounded by cells of varying number which are indistinguishable in form or position from the remainder of the epidermal cells (FIG. 10). Guard cell walls are thickened along the inner surface facing the spongy mesophyll and on the outer surface (FIGS. 11, 12). In paradermal view, guard cells are elongate-reniform (FIG. 10).

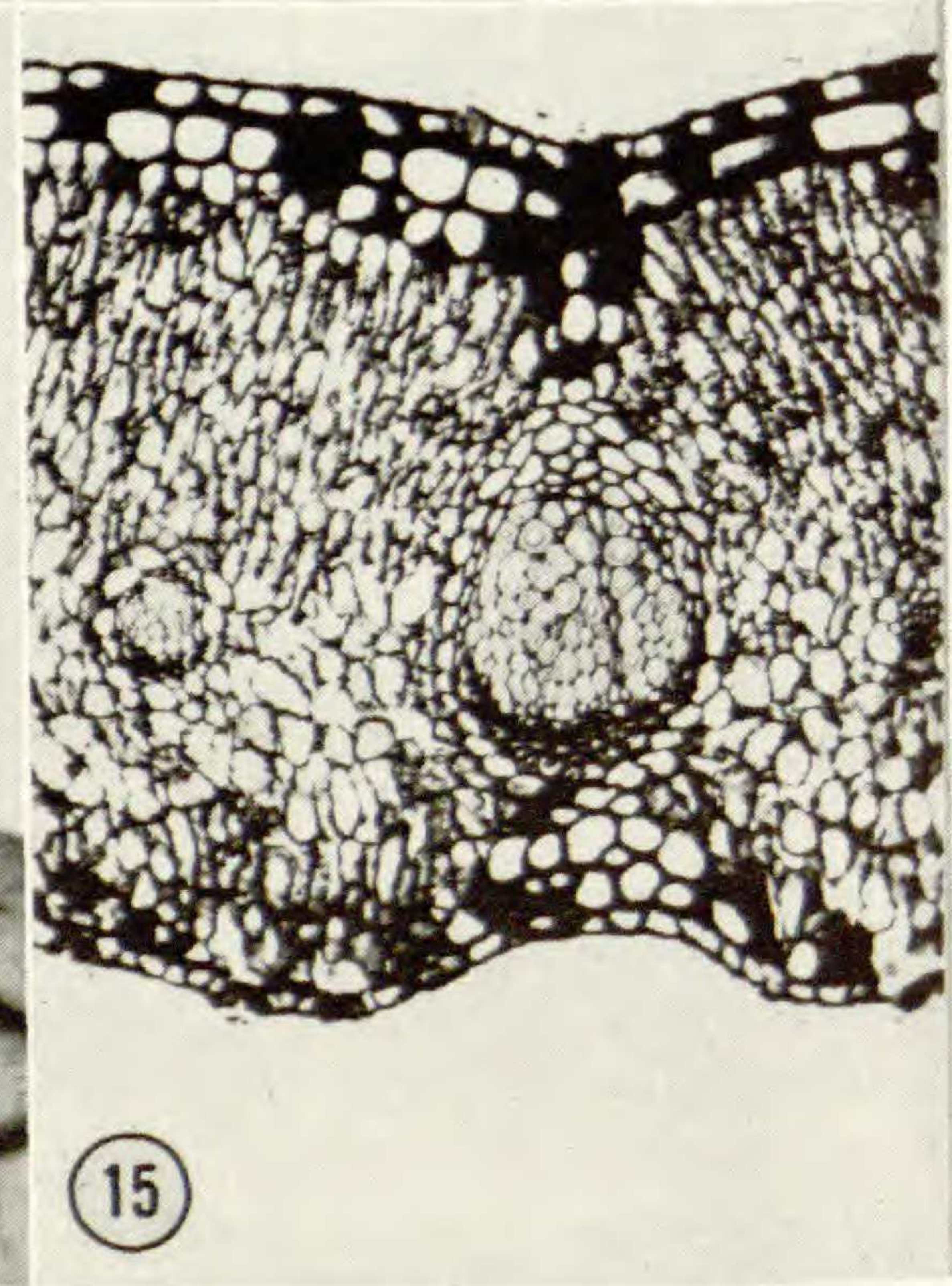
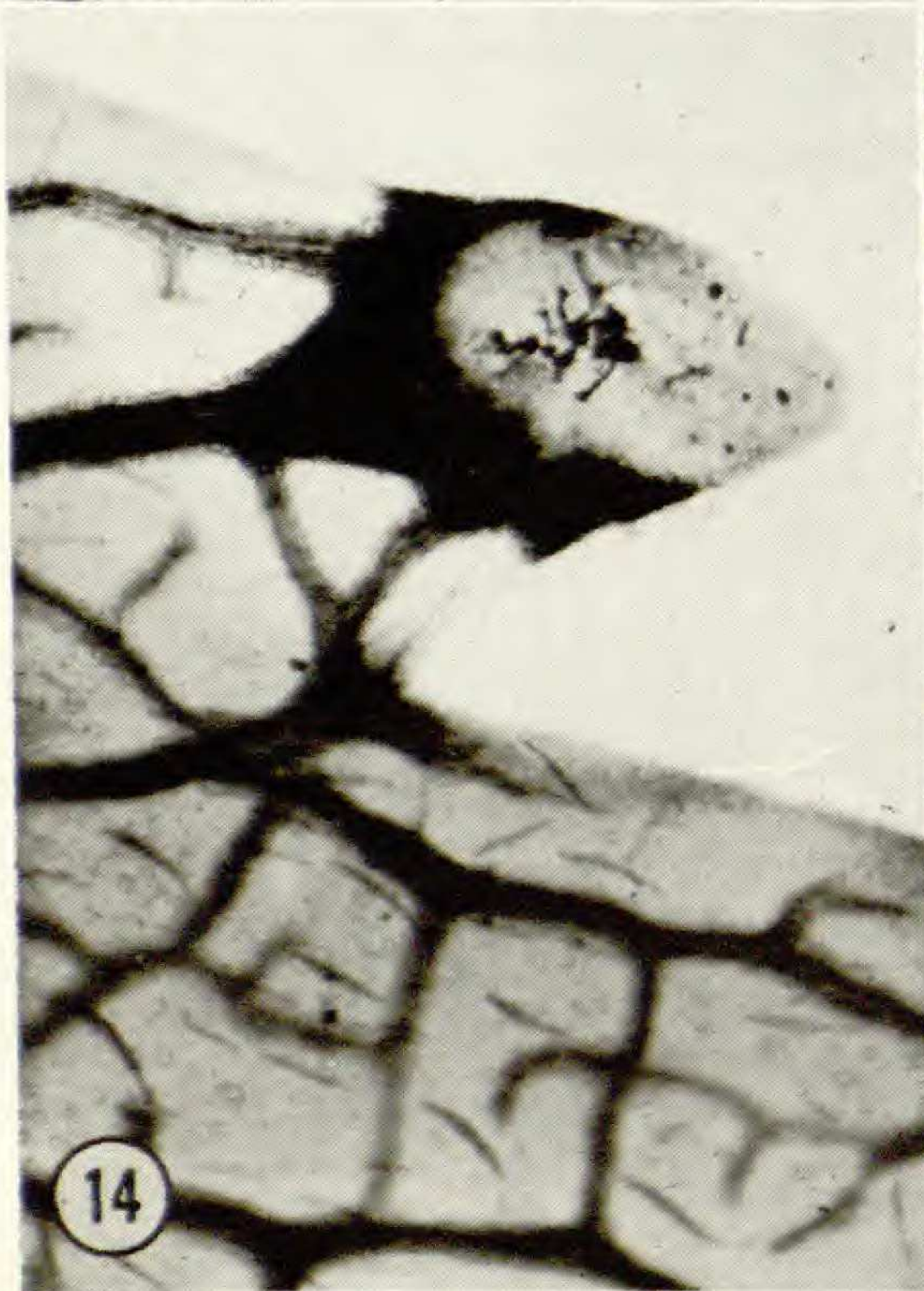
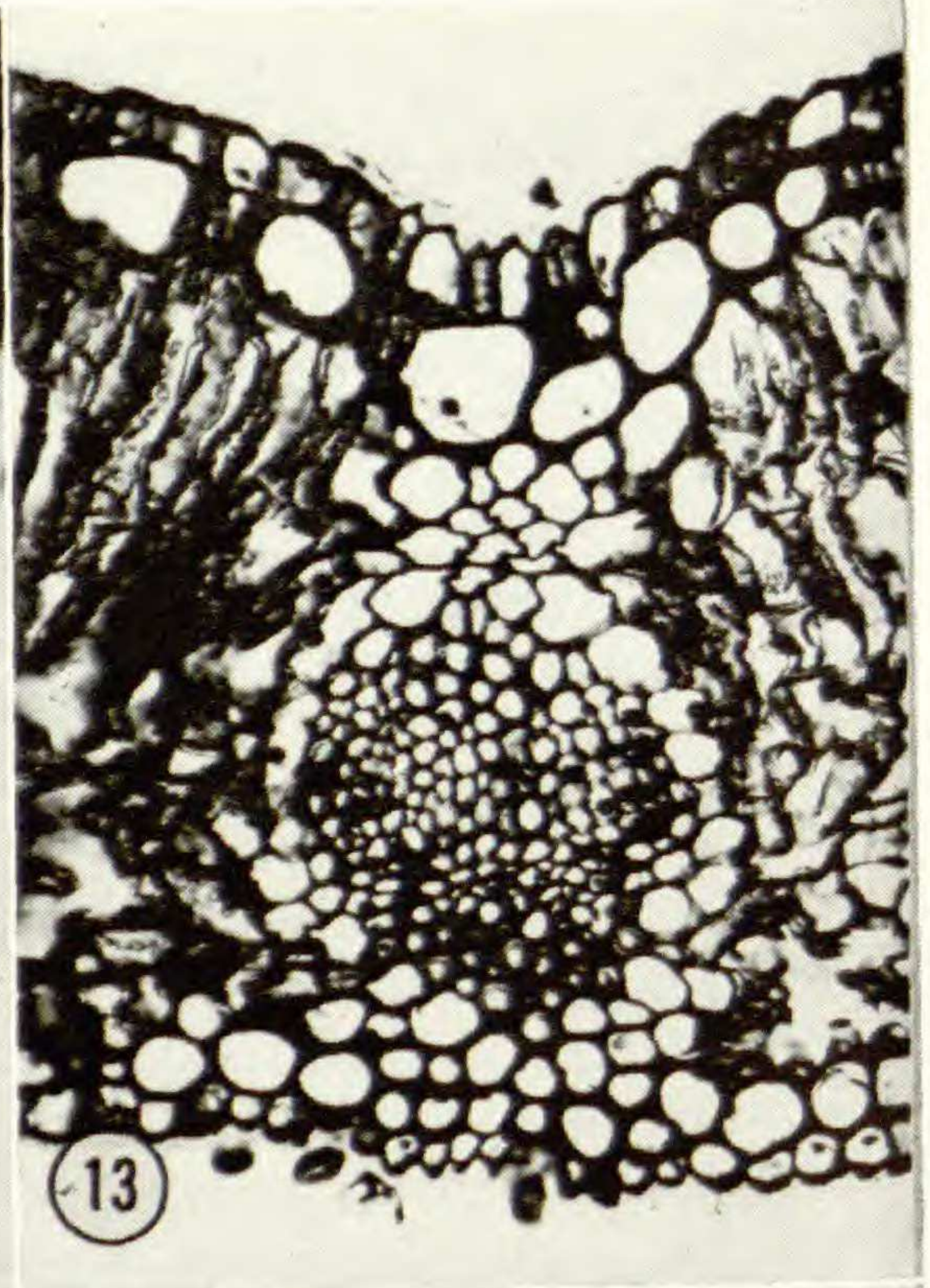
The lower epidermis is uniseriate; the upper epidermis is biseriate (FIGS. 11, 13, 15). Since developmental studies could not be conducted, it is not possible to determine if the inner layer is protodermal in origin or if it arose from the ground tissue. Inner cells of the biseriate upper epidermis are larger and conspicuously more rotund than those of the outer layer (FIGS. 13, 15). Leaves are dorsiventral and the mesophyll is divided into a biseriate, upper palisade layer and a lower spongy layer. In the thickish leaves of *Columellia lucida* and *C. obovata*, the transition between palisade and spongy mesophyll is not sharp. Furthermore, in these two species, there is a tendency for a lower palisade layer to be formed and an isobilateral condition (FIG. 15).

Leaves of all species of *Columellia* are glandular; in those species having serrate leaves, the tips of the teeth and the apical point are glandular; in species with entire leaves, the apex of the leaf may be glandular.

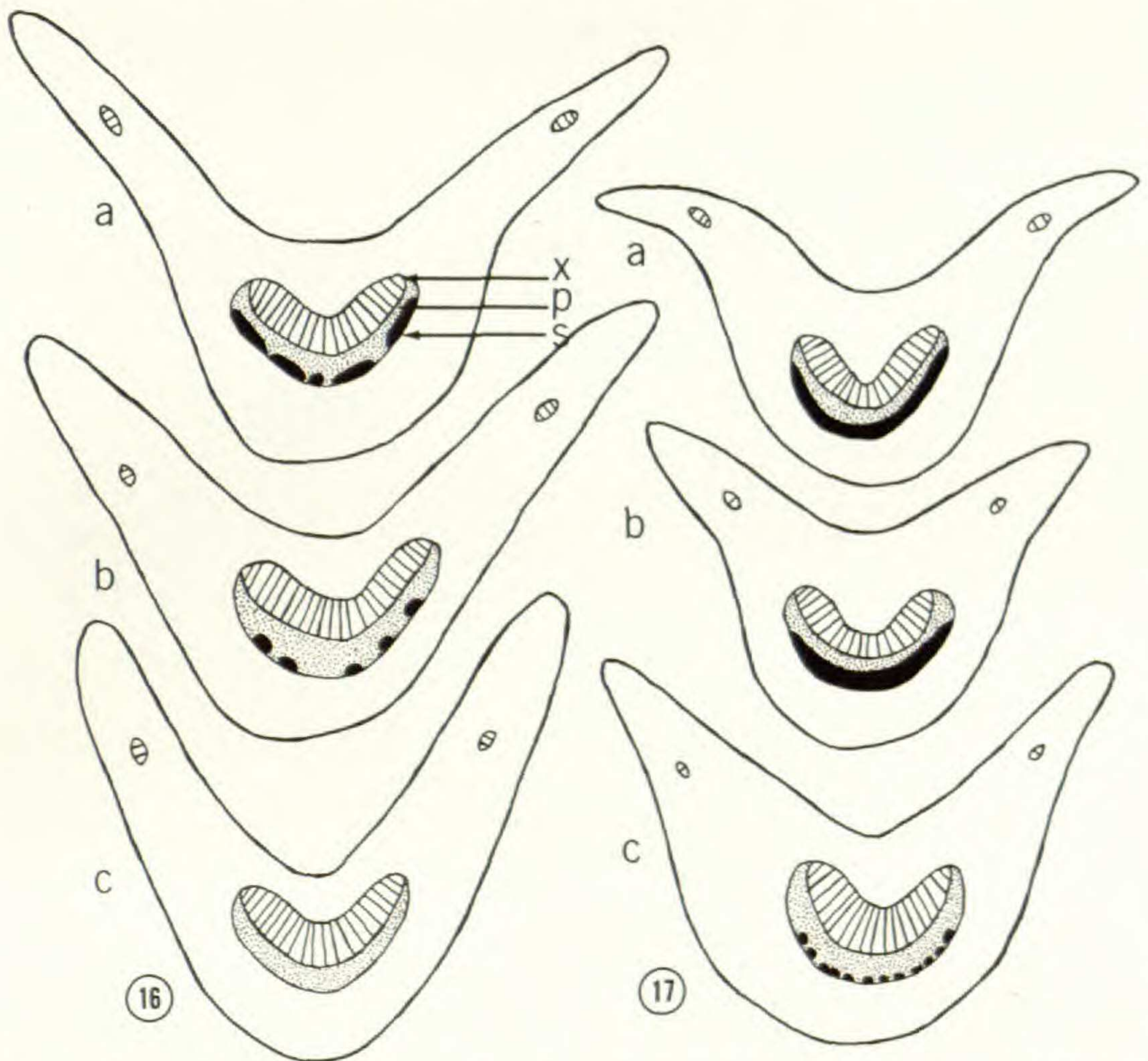
<sup>2</sup> Although Metcalfe and Chalk (1950), Fahn (1967), and Esau (1965) do not agree, the first author would prefer to use the term *stoma* (Gr. a mouth) in its restricted sense to mean the actual aperture or pore in the epidermis which is surrounded by the guard cells. The term *stomatal apparatus* is used here to mean the stoma, guard cells, and subsidiary (accessory) cells, if present. The maintenance of separate terms for the aperture and guard cells seems meritorious in that it provides for independent reference to each of these units and alleviates the possible redundant implications of referring to the "aperture of a stoma."



FIGS. 10 and 11. *Columellia oblonga* ssp. *oblonga*, *Továr* 4033. FIG. 10. Paradermal view of leaf epidermis showing elongate-reniform guard cells and thick-walled hairs set into saucer-like depressions. FIG. 11. Transverse section of leaf showing biseriate upper epidermis, biseriate palisade layer, and uniseriate lower epidermis. The cuticle overarches the unevenly thickened guard cells externally and internally to form front and back cavities. Bases of hairs are situated in saucer-like depressions of the lower epidermis.



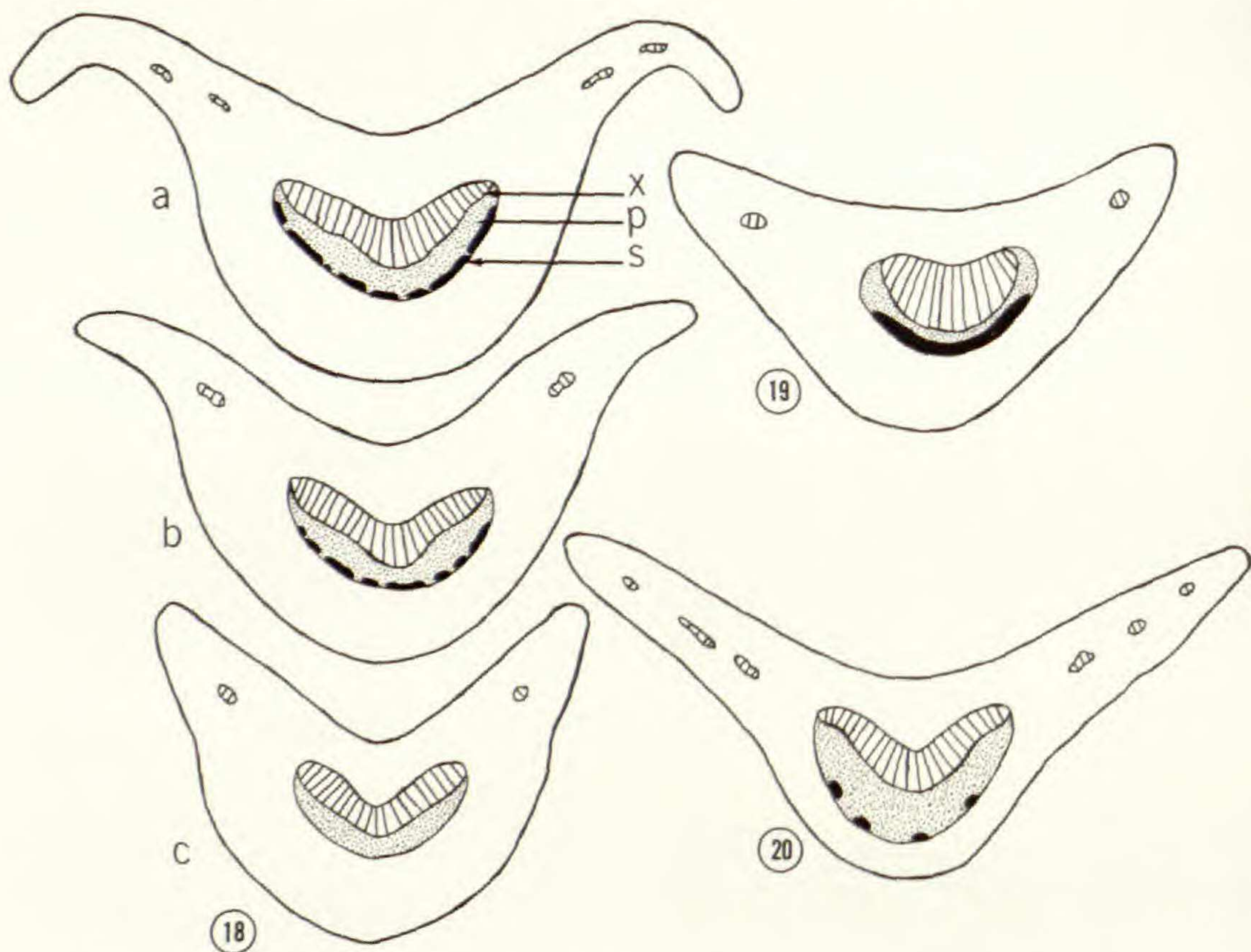
FIGS. 12-15. FIG. 12. *Columellia lucida*, Friedberg 240, transverse section of lower epidermis of leaf showing thickened cuticle and overarching cuticular modification in association with stomatal apparatus,  $\times 600$ . FIG. 13. *C. oblonga* ssp. *oblonga*, Továr 4033, transverse section through mid-vein of leaf showing biseriata upper epidermis, uniseriate lower epidermis, bundle sheath, and bundle sheath extensions,  $\times 210$ . FIG. 14. *C. oblonga* ssp. *oblonga*, Továr 3785, cleared whole mount of leaf showing a single glandular serration; dark bodies in gland are fruiting structures of an aspergillous fungus,  $\times 40$ . FIG. 15. *C. lucida*, Friedberg 240, transverse section through mid-vein of leaf showing biseriata upper epidermis, uniseriate lower epidermis, bundle sheath and bundle sheath extensions, tendency to development of a lower palisade layer, and abundance of thick-walled fibers in the vascular bundle,  $\times 180$ .



FIGS. 16 and 17. Sectional series through petioles of *Columellia*, (a) being distal, (c) proximal, showing increasing distal development of sclerenchyma. FIG. 16. *C. oblonga* ssp. *sericea*, Drew E-113. FIG. 17. *C. oblonga* ssp. *oblonga*, Cook & Gilbert 1749. (x) xylem, (p) phloem, (s) sclerenchyma.

Glands are highly vascularized and massive (FIG. 14); proximally adjacent to the secretory epithelium is a cupulate reticulum of vascular elements. That the central portion of the gland contains a cavity is borne out by the occurrence there of aspergillous fruiting bodies in some specimens. Apices of glands are aperturate probably through schizogeny.

Vasculature of the petiole is characterized by a single collateral strand of conducting tissue varying from crescentiform to cupulate to almost semiterete in transverse section (FIGS. 16-20). Xylem is adaxial and phloem is abaxial. In all species examined, an abaxial sclerenchymatous region develops progressively from the proximal to the distal portion of the petiole (FIGS. 16-18). In specimens of *Columellia oblonga* ssp. *oblonga* (FIG. 17) and *C. lucida* (FIG. 19), a well-developed lunate layer completely subtends the phloem at the extreme distal end of the petiole; in specimens of other species (FIGS. 16, 18, 20) the sclerenchyma seems not to develop into more than a series of widely-spaced rods at this point. However, sections through the mid-vein of the lamina in *C. oblonga* ssp.



FIGS. 18-20. FIG. 18. *Columellia oblonga* ssp. *serrata*, Bang 1172, sectional series through petiole, (a) being distal, (c) proximal, showing increasing distal development of sclerenchyma. FIG. 19. *C. lucida*, Friedberg 240, distal section of petiole showing complete sclerenchymatous arc. FIG. 20. *C. obovata*, Vargas 7693, distal section of petiole showing sclerenchyma as an arc of rods at this point. (x) xylem, (p) phloem, (s) sclerenchyma.

*sericea* (Drew E-113), which shows a series of sclerenchymatous rods at the distal end of the petiole (FIG. 16, a), show a complete sclerenchymatous layer subtending the phloem. It is likely, therefore, that in the laminae of all species of *Columellia*, the mid-vein is supported by an abaxial layer of sclerenchyma. The central vascular strand of the petiole branches into a series of minor strands toward the base of the lamina (FIGS. 16-20).

In *Columellia oblonga* the mid-vein of the lamina is characterized by secondary growth and several layers of secondary xylem and phloem are produced (FIG. 13). In *C. lucida* and *C. obovata*, secondary growth is not pronounced; furthermore, in these species most of the xylem in the mid-rib and secondary veins consists of thick-walled fibers (FIG. 15). Bundle sheaths surround secondary veins in all species. Bundle sheath extensions (Wylie, 1952) reach upper and lower epidermises in *C. oblonga* (FIG. 13); in *C. lucida* and *C. obovata*, there are no bundle sheath extensions associated with the bundle sheaths of secondary veins.

The node in *Columellia* is unilacunar and a single trace emerges through each of the two opposite gaps in the vascular cylinder (FIG. 21).



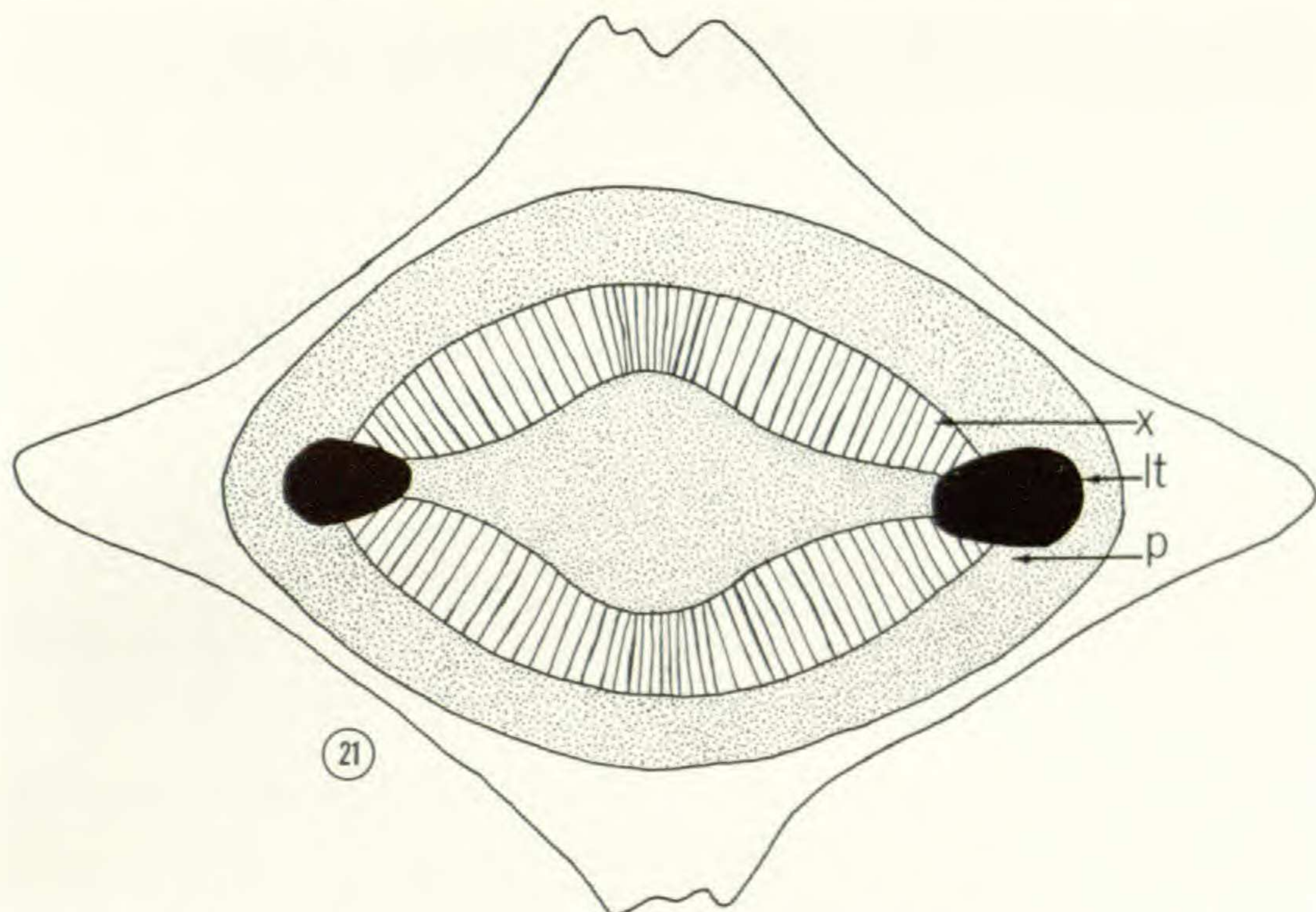


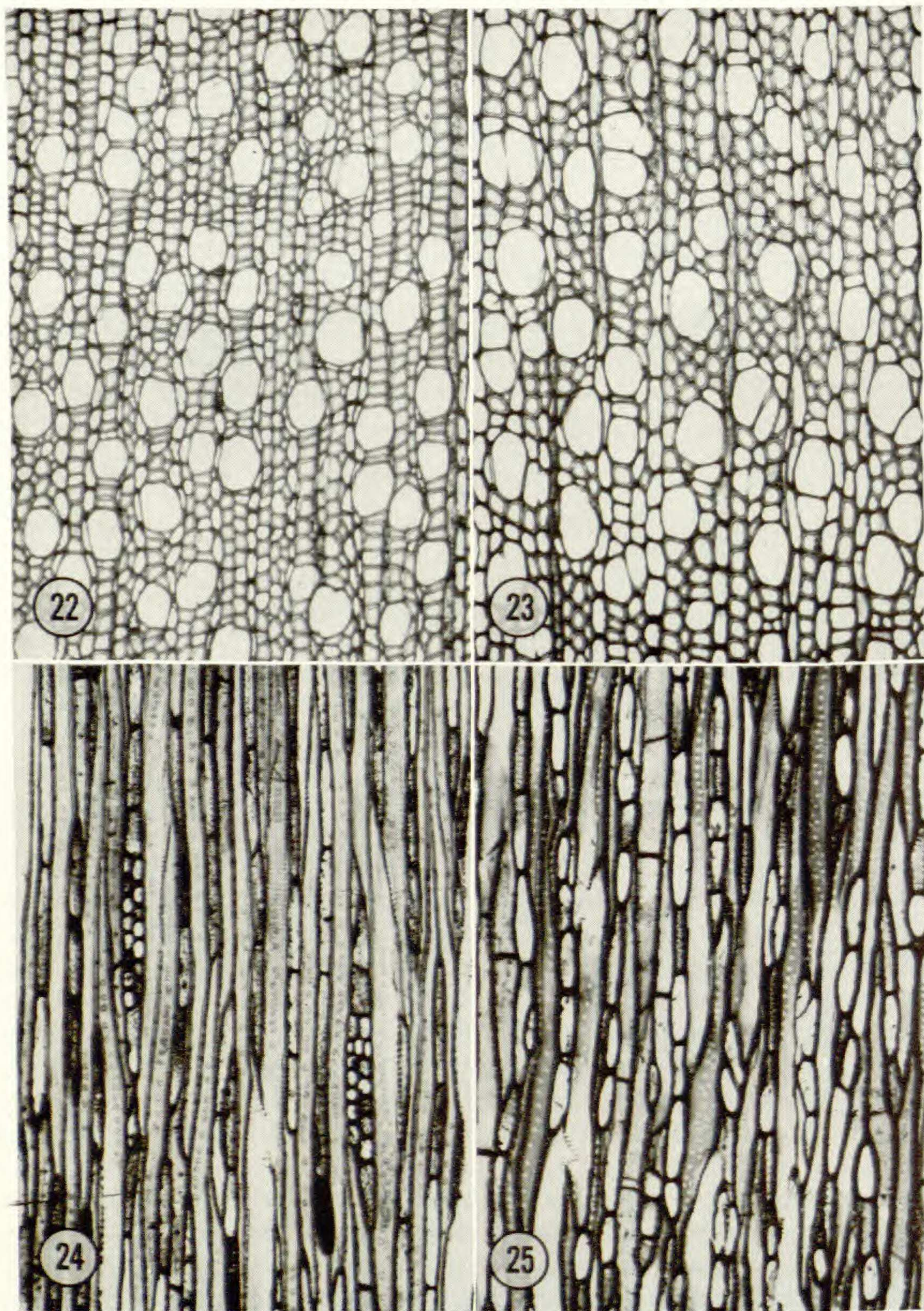
FIG. 21. Transverse section of stem illustrating the unilacunar node in *Columellia*; (x) xylem, (p) phloem, (lt) leaf trace.

#### The secondary xylem

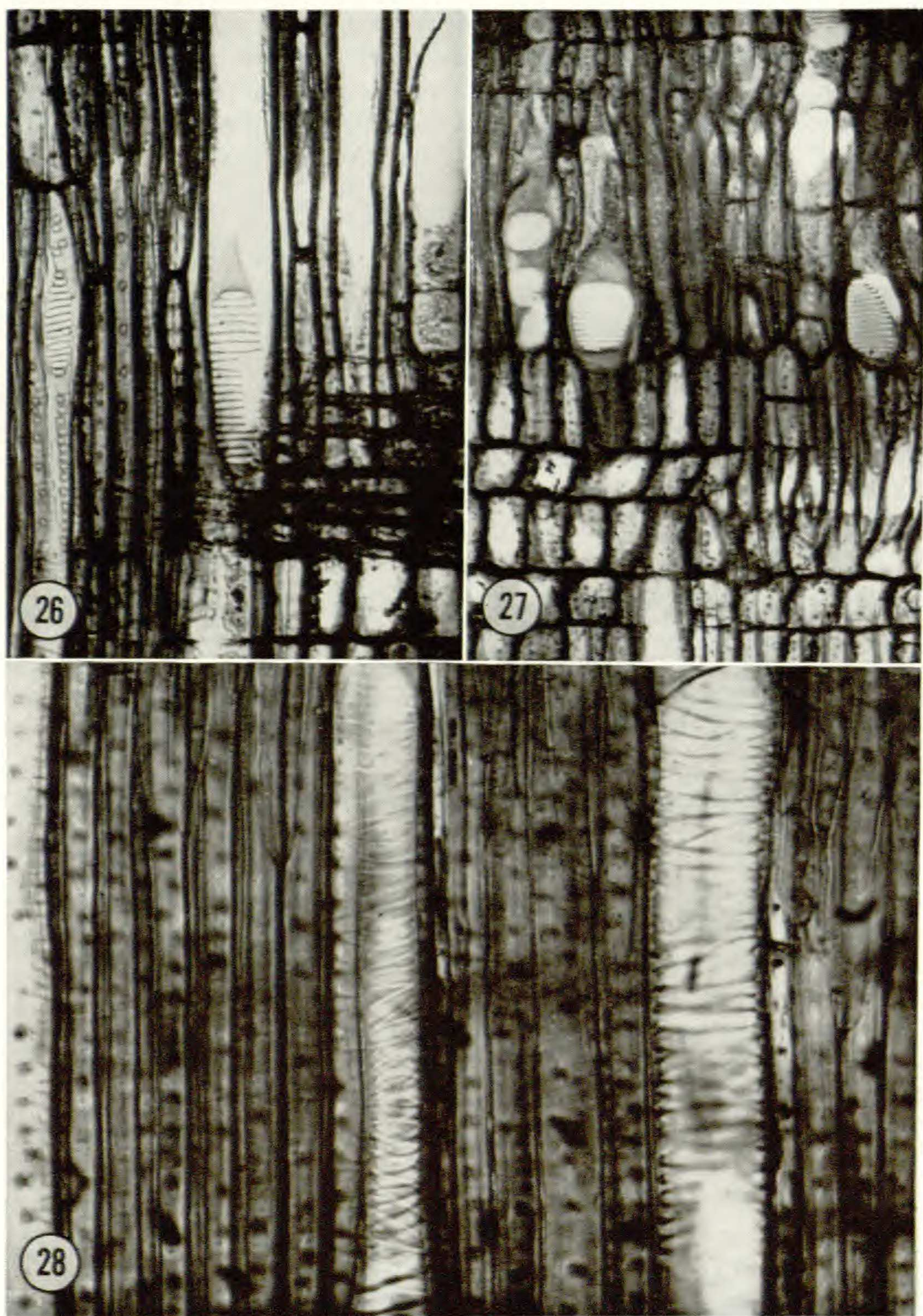
The wood of *Columellia* is generally without growth rings, although in the immature specimens of *C. obovata*, represented by *Weberbauer 5482* and *Nuñez 3309*, more or less sharply defined rings occur. However, both of these specimens show strong evidence of decay or disease and it is suspected that the growth rings are related to these conditions. All woods examined are diffuse-porous, the strictly solitary, uniformly-sized pores being distributed evenly across the transverse surface (FIG. 23). Vessel walls are thin and there are no tyloses. Pores are angular.

Data for measurements of vessel diameter, vessel element length, bars per scalariform perforation plate, tracheid length, and heights of vascular rays are presented in TABLE 2. Because both mature and immature wood were examined, measurements for each are separated in the table to provide a more meaningful basis for comparisons with xylem in other taxa.

Vessel elements are generally long and narrow although ligules as such are short and sometimes lacking. End wall angle ranges from  $10^{\circ}$  to  $45^{\circ}$ . Perforation plates are entirely scalariform (FIG. 27) and in some cases bars are so profusely branched they give the appearance of pits. Openings in scalariform perforation plates are completely bordered. Spiral thickenings occur in the cell walls of ligules throughout all species, being more prominent in some than in others. In specimens of *Columellia oblonga* ssp. *oblonga*, vaguely outlined spirals are seen in the body segment of vessel elements and they are strongly marked in the ligules; in *C. oblonga*



FIGS. 22-25. FIG. 22. *Escallonia myrtilloides*, Rimbach 13, Yw 16920, transverse section of xylem showing solitary distribution of angular pores,  $\times 100$ . FIG. 23. *Columellia oblonga* ssp. *sericea*, Rimbach 122, transverse section of xylem showing solitary distribution of angular pores, and scanty vasicentric and diffuse axial parenchyma,  $\times 100$ . FIG. 24. *E. myrtilloides*, tangential section of xylem with biseriate vascular rays and spiral thickenings in tracheids and vessels,  $\times 100$ . FIG. 25. *C. oblonga* ssp. *sericea*, tangential section of xylem showing uniseriate vascular rays and tracheids,  $\times 100$ .



FIGS. 26-28. FIG. 26. *Escallonia myrtilloides*, Rimbach 13, Yw 16920, radial section of xylem showing scalariform perforation plates,  $\times 150$ . FIG. 27. *Columellia oblonga* ssp. *sericea*, Rimbach 122, radial section of xylem showing scalariform perforation plates,  $\times 100$ . FIG. 28. *C. obovata*, Weberbauer 5482, longitudinal section of xylem showing spiral thickenings in vessels,  $\times 500$ .

ssp. *sericea*, spirals are tenuous at best and appear only in ligular portions; in *C. lucida* spirals occur only in ligules; and in *C. obovata* spirals are conspicuous throughout the lengths of vessel elements (FIG. 28).

Intervascular pitting is generally absent owing to the solitary nature of vessels; however, a suggestion of intervacular pitting is sometimes present in the overlapping ends of superposed vessel elements. In these areas, the circular to elongate pits are sparse and irregularly scattered but there is a tendency toward the alternate arrangement.

Imperforate tracheary elements are tracheids, the pits in these cells being of the same order of magnitude as those which occur in the overlapping ligulate portions of vessel elements (FIG. 25). Pitting in tracheids is ordinarily uniseriate; less commonly two rows of pits are present, staggered alternately. Inner apertures of pits are elliptical, crossed in face view, and included within the pit border. Tracheid walls vary from very thin to thick.

Vascular rays are entirely uniseriate and comprise axially elongated or upright cells only (FIG. 25). These rays are homocellular and the ray tissue corresponds with Kribs' (1935) Heterogeneous Type III.

TABLE 2.

## Summary of Xylem Anatomical Measurements in Columelliaceae

	MATURE <sup>a</sup>	IMMATURE <sup>b</sup>
VESSEL DIAMETER IN $\mu$		
Average:	45	25
Range:	22-105	12-45
MFR <sup>c</sup> :	30-70	15-36
VESSEL ELEMENT LENGTH IN $\mu$		
Average:	629	
Range:	308-1100	
MFR:	375-828	
BARS PER SCALARIFORM PERFORATION PLATE		
Average:	14	10
Range:	7-20	3-24
MFR:	11-16	6-17
TRACHEID LENGTH IN $\mu$		
Average:	866	
Range:	378-1260	
MFR:	625-1110	
HEIGHT OF VASCULAR RAYS IN CELLS		
Range:	1-6	1-47+

<sup>a</sup> *Columellia oblonga* ssp. *oblonga*, Továr 4033, Wurdack 1732. *C. oblonga* ssp. *sericea*, Rimbach 122 and 30.

<sup>b</sup> *Columellia oblonga* ssp. *oblonga*, Ruiz & Pavón 1/52; Weberbauer 5584 and 7791. *C. lucida*, André K-1444 and 4500. *C. obovata*, Weberbauer 5482, Herrera 3451. Data from Nuñez 3309, a diseased specimen, are not included here.

<sup>c</sup> MFR = Most frequent range.

Axial xylem parenchyma is largely scanty vasicentric, a few isolated strands occurring about the vessels (FIG. 23). In addition a few strands were seen embedded within the groundmass of tracheids (diffuse parenchyma).

## DISCUSSION

In view of the sympetalous corolla of *Columellia*, it is not surprising that taxonomists looked for its relationships among the sympetalous families, and especially those with inferior ovaries and opposite leaves. Among other features, the androecial peculiarities of *Columellia*, unmatched in any other known taxon, persuaded David Don to establish a separate family for this unusual group of plants. Time has shown him to have been correct in his assessment of the individuality of *Columellia*.

### Evidence from gross morphology

There are such sharp differences in floral structure between Columelliaceae on one side, and Ebenaceae, Styracaceae, and Vacciniaceae on the other, that any consideration of close relationship is completely out of place. Oleaceae, with usually 2-4-merous flowers, 2 (-4) stamens with introrse, dorsifixed anthers, and superior ovaries with a few ovules situated on an axile placenta in each locule, can hardly be regarded as closely related to Columelliaceae. The mostly herbaceous Gentianaceae-Gentianoideae show some similarities with Columelliaceae in their cymose inflorescences, in the structure of ovaries and fruits (2-carpellate ovaries with numerous unitegmic, tenuinucellate ovules on parietal intrusive to axile placentas, septicidal capsules, small seeds, etc.), as well as in the possession of opposite, exstipulate leaves. They are markedly different, however, in their regular flowers; in the usually contorted aestivation of corolla lobes; in their usually dorsifixed, introrse anthers; and in their superior ovaries. Loganiaceae (excluding *Desfontainea* Ruiz & Pavón) differ from Columelliaceae in their usually stipulate leaves, regular flowers, and superior ovaries; in addition, in the subfamily Buddleioideae, the presence of glandular and stellate hairs is widespread. Some relationship with Scrophulariaceae and especially Gesneriaceae appears possible, but both families have highly specialized, mostly hypogynous flowers (only Gesnereae of Gesneriaceae, *sensu* Fritsch 1893, 1894, have semi-inferior or inferior ovaries). Some genera of Rubiaceae agree with Columelliaceae in floral structure (except for the non-reduced number of stamens) and opposite leaves, but they differ in the presence of stipules. A close relationship with Caprifoliaceae seems equally doubtful. The only genera of this family which are perhaps comparable with Columelliaceae in possessing multi-ovulate, 2-carpellate ovaries, are *Diervilla* Mill. and *Weigela* Thunb., genera apparently restricted to the temperate zones of North America and eastern Asia. The gross-morphological similarities between Lythraceae and Onagraceae and Columelliaceae are too scarce even to suggest a relationship. Within the saxifragaceous families —

Hydrangeaceae, Grossulariaceae, and Escalloniaceae — almost all the gross-morphological characters in *Columellia* may be found: frutescent and/or arborescent habit; opposite, exstipulate, often glandular-dentate leaves; 5-merous haplostemonous flowers (Escalloniaceae); sympetalous corolla (*Roussea* of Escalloniaceae); and semi-inferior or inferior, 2-carpellate ovaries with parietal intruding placentas bearing numerous, anatropous and apotropous, unitegmic, tenuinucellate ovules (Escalloniaceae and some genera of Hydrangeaceae). Septicidal capsules usually have numerous small endosperm-containing seeds (Hydrangeaceae and Escalloniaceae) with small embryos. Most of the features of *Columellia* are represented in the family Escalloniaceae. Although alternate leaves predominate in this family, opposite leaves are found in the genera *Grevea* Baill., *Roussea*, and *Polyosma* Blume. Other genera, as *Valdivia* Remy, have subopposite leaves.

#### Evidence from floral anatomy

It would not be practical, nor is it necessary, to attempt a detailed anatomical comparison of the *Columellia* flower to flowers of all the plant families with which *Columellia* has been allied. A brief commentary on the Cucurbitaceae seems to be in order, however, because androecial structure in that family has significance for the interpretation of the androecium in *Columellia*.

Clarke (1858) considered the stamens of *Columellia*, because of their contorted anthers, to be almost identical to those of many Cucurbitaceae. He interpreted the androecia of certain cucurbits — those with three appendages, one two-locular and two four-locular — as comprising two and a half stamens, an opinion shared by some other 19th century botanists. If this view were correct, the two-staminate androecium of *Columellia* would not seem greatly different. In more recent times, however, an alternative interpretation of such cucurbitaceous androecia has been confirmed again and again; that is, the two-sporangiate stamen is an entire one, and the four-sporangiate stamens are duplex appendages. Evidence for the more modern view is now overwhelming. It is derived from ontogeny; from vascular anatomy (the duplex stamens sometimes contain two well-defined bundles that are derived from two different petal traces); and from comparative studies of male, female, and bisexual flowers of many genera, some of them exhibiting transitional stages between the five-staminate condition and the "two and a half"-staminate condition. Reviews of the evidence are given by Miller (1929) and McLean (1947) and additional confirmation by Bhattacharjya (1954), Chakravarty (1958), and Quang (1963).

Although *Columellia* stamens are superficially similar to the duplex stamens of Cucurbitaceae, the vascular supply in *Columellia* is a solitary bundle. In transverse sections through the filament or the connective, the bundle is often very broad and may occasionally seem to have two xylem patches, but its appearance within the inferior part of the flower gives no

hint of compound structure. Observing this, van Tieghem (1903) concluded that the two members of the *Columellia* androecium are solitary stamens, and most floral morphologists would accept his evidence. Thus, it can be argued rather convincingly that the evolutionary modification leading to the two-staminate condition in *Columellia* was a loss or "abortion" of stamens rather than any sort of phylogenetic union of stamens. The occasional occurrence of a third stamen in flowers of *Columellia*, reported by Brizicky (1961), supports this argument.

This reasoning might be thought to favor the relationship of *Columellia* to Gesneriaceae, because some gesneriads have one staminode — that is, an abortive stamen — accompanying four normal stamens, and in some other gesneriads there are only two stamens. In the latter case, as in *Columellia*, there are no staminodes. But the resemblance of *Columellia* to the gesneriads is not so close as this information would suggest, for in Gesneriaceae only genera with superior ovaries have the two-staminate androecium (Fritsch 1893, 1894).

A satisfactory anatomical comparison of the *Columellia* flower with gesneriaceous flowers is not yet possible because floral anatomy of the Gesneriaceae has never been investigated to any great extent. Comparative information is presently available only for flowers of a *Kohleria* hybrid, *K. amabilis* × *K. scladotydea* (Teeri, 1968), and for those of *Kohleria elegans* (Dcne.) Loes. (*H. E. Moore* 8190; US, BH). Serial sections of the latter were prepared from fluid-preserved material especially for this paper. Anatomically, flowers of the two gesneriads are much alike, and they have several characters in common with *Columellia*. For instance, the floral tissues are devoid of tannins, and general features of placentation and vasculature do not differ greatly from those of *Columellia*. In addition, both gesneriads have two-lobed placentas and many gynoeical strands (FIG. 8). On the other hand, there are differences in detail that may be important. The two gesneriads have no well-developed endocarp tissue, except for a single layer of transversely elongate cells adjoining the locule. The style is hollow for all of its length, with a single canal (FIG. 5). Floral trichomes are multicellular (but uniseriate). Vascular traces to the stamens are united with sepal traces for part of their passage through the inferior part of the flower, and the supply to the placentas is derived from two large septal bundles (duplex bundles representing paired heterocarpous ventrals; FIG. 9) in the septum. Of course, a major floral difference is that the anthers of the gesneriads are not contorted. Perhaps the most important difference aside from that is in the nectary: nectaries of Gesneriaceae are usually very well developed and deeply lobed or even divided into distinct appendages (Feldhofen 1933).

It is somewhat easier to compare flowers of *Columellia* with those of Rubiaceae because a detailed survey of floral anatomy in Rubiaceae is available (Rao, Ramarethinam, & Iyer 1964). Rubiaceae is a large family, rather diverse in floral structure; therefore, it is almost to be expected that some of the members would have characters in common with *Col-*

*umellia*. For instance, some Rubiaceae have separate vascular traces to calyx, corolla, androecium, and gynoecium. And in some genera (e.g., *Guettarda* L.) there are a great many gynoecial bundles. Placentation is often similar to that of *Columellia*, and many genera have an epigynous nectary resembling that of *Columellia*. A difference that strikes one immediately, when sectioned flowers of *Columellia* are compared with sections of rubiaceous flowers, is the absence of conspicuous tannins in the former. Floral tannins are rarely lacking in Rubiaceae. Another difference is that a single stylar canal seems to be of universal occurrence in the Rubiaceae. Furthermore, the peculiar androecial modification in *Columellia* has no counterpart among the rubiads.

Floral anatomy of the more easily obtained members of Saxifragaceae, *sensu lato*, is fairly well known through the investigations of many workers, including Palmatier (1943), Morf (1950), Dravitski (see Philipson, 1967), Gelius (1967), and Komar (1967). None of these studies has produced evidence to support Hallier's (1908, 1910) opinion that *Columellia* belongs with the Philadelphae. In fact, ontogenetic observations on *Philadelphus* (Gelius, 1967) suggest that evolution has favored an increase in stamen number in this group. In some other genera of Philadelphae, a reduction in the number of ovules has led to forms that bear little resemblance to *Columellia* (e.g., *Jamesia* Torr. & Gray, *Whipplea* Torr.). Schnizlein (1843–1870) proposed *Brexia* and *Roussea* as close allies of *Columellia*; however both *Brexia* and *Roussea* have superior ovaries with distinctly two-ranked ovules. *Argophyllum*, another genus mentioned by Schnizlein, is also very dissimilar to *Columellia*, for it has peculiar corolline ligules and T-shaped trichomes like its ally *Corokia* A. Cunn. (Eyde, 1966). If the relationships of *Columellia* are to be sought among the escalloniods, attention should be given to genera other than the aberrant *Argophyllum* and *Corokia*. *Berenice* Tul. can also be eliminated from consideration, because it has recently been transferred to Campanulaceae on anatomical and palynological grounds (Erdtman & Metcalfe, 1963). From the standpoint of floral anatomy, *Escallonia* Mutis ex L. f. is not as close to *Columellia* as might be indicated by other evidence. Tannins are abundant in floral tissues of *Escallonia* species and the floral trichomes frequently are multicellular with globular terminal portions; also, the gynoecial bundles are few and the ventral bundles commonly accompany the dorsals into the style. *Choristylis* Harv. has stamens united with corolla tube, but in other respects the flowers are unlike those of *Columellia*. One difference is that the gynoecial bundles are few; another is that the nectary is located on the lower part of the corolla tube. The latter character may be sufficiently important to remove *Choristylis* from its position adjoining *Forgesia* (Engler, 1928) and to place it elsewhere in the Saxifragaceae, *sensu lato*. (Agababyan 1964, links *Choristylis* with *Itea* on palynological evidence.) Flowers of *Forgesia* have rather massive multicellular trichomes; otherwise they are anatomically similar to *Columellia* flowers. To judge from our one sectioned her-



barium flower, the gynoecial vasculature and the placentation approximate those of *Columellia*. The nectary, if there is one (it is not easy to tell from dried material), is part of the free portion of the gynoecium, and the androecium shows indications of reduction (abortive locules in some anthers). *Forgesia*, like many other Saxifragaceae, *sensu lato*, has free styles that could be viewed as a precursor to the two-canal structure of the *Columellia* style.<sup>3</sup>

In summarizing this section on floral anatomy, it must be conceded that the cited points of similarity and dissimilarity do not tell us much about the affinities of *Columellia*. The foregoing commentary includes no strong evidence against the proposed relationship with Gesneriaceae, nor does it include really firm evidence for such a relationship. The same can be said of the possible alliance with Rubiaceae or with the escallonioid group of Saxifragaceae, *sensu lato*. The reason for this is clear. All observed characters in the flowers of *Columellia* are widely distributed in many plant families, except for the contorted anthers. Ironically, the latter character does not help in placing *Columellia* because it has not been found in any other group of plants, the resemblance to anthers of certain cucurbits being demonstrably superficial.

#### Evidence from leaf anatomy

It does not appear possible to compare all features of the foliar anatomy of Columelliaceae with those of families reputed to be allied to it, since complete foliar surveys of these families are lacking from the literature. An original study of leaves in all these families is surely outside the scope of this investigation. Nevertheless, certain comparisons can be made.<sup>4</sup>

Leaves are dorsiventral in Gesneriaceae. Hairs are always multicellular and they are often situated on a pedestal. They may be glandular or non-glandular. A multiseriate hypodermis occurs in certain species. The stomatal apparatus is often very large and anisocytic. Vascular bundles in veins are not usually accompanied by sclerenchyma. Vasculature of the petiole is various and many genera show a single leaf trace; *Alloplectus* Mart., *Besleria* L., *Episcia* Mart., and others have three leaf traces and *Klugia notoniana* A. DC. shows a large number of separate strands. There is no "pericyclic" sclerenchyma associated with the petiolar vascular strand in Gesneriaceae. Gesneriaceous leaves differ markedly from those in Columelliaceae in their multicellular and glandular hairs, anisocytic stomatal apparatus, and lack of sclerenchyma associated with vascular tissue.

<sup>3</sup> Observations on the floral anatomy of Escalloniaceae are based on serial sections prepared especially for this paper. Material was obtained from the following sources: *Escallonia*, fluid-preserved flowers from several cultivars growing in the Los Angeles State and County Arboretum, not vouchered; *Carpodetus serratus*, fluid-preserved flowers from plants cultivated at the University of Auckland, New Zealand, not vouchered; *Quintinia fawkneri*, pressed flowers, L. J. Brass 4719, US; *Choristylis shirensis*, pressed flowers, Swynnerton 607, US; *Forgesia borbonica*, pressed flowers, de l'Isle 216, US.

<sup>4</sup> Family circumscriptions follow those used by Metcalfe and Chalk (1950) for convenience in making comparisons.

Rubiaceous leaves are generally dorsiventral; centric and homogeneous leaf organization occur in a few species. Hairs may be unicellular, multicellular and uniseriate, tufted, and rarely peltate. A hypodermis occurs in many species. The stomatal apparatus is paracytic (rubiaceous) in most species, as might be expected. The petiolar vascular strand is usually shield shaped with more or less well-developed wings. There are also variously shaped median vascular strands, nearly always associated with smaller accessory bundles toward the wings. In such a large and anatomically diverse family as Rubiaceae, it is not surprising to find foliar resemblances to Columelliaceae. The only clear and consistent difference is the more or less ubiquitous occurrence of the paracytic stomatal apparatus in Rubiaceae.

Caprifoliaceae usually have dorsiventral leaves, but the palisade tissue is poorly developed in species of *Triosteum* L. and *Viburnum* L. Hairs may be glandular or non-glandular and unicellular, simple and multiseriate, tufted or stellate, and peltate. Glandular leaf teeth are present in some species. Stomatal organization is frequently anomocytic, but paracytic types occur in the same genera as anomocytic types. Except for *Diervilla*, a single layer of palisade mesophyll occurs; in *Sambucus* L. and *Viburnum*, cells of the palisade layer may have arms. The petiolar vasculature shows a considerable range of structure from a solitary, slightly crescentic bundle to an arc of 3–5 or more separate bundles to a closed vascular cylinder. The anomocytic stomatal apparatus and solitary petiolar strand in Caprifoliaceae are similar to Columelliaceae, but the paracytic stomatal apparatus, single-layered palisade mesophyll, and multi-strand and cylindrical vasculature of the petiole, which also occur in some species of Caprifoliaceae, are very different from the situation in Columelliaceae.

Leaves in Saxifragaceae, *sensu stricto*, are dorsiventral and isobilateral. Hairs are glandular and non-glandular and these may be simple, uniseriate and multicellular; shaggy; and multiseriate. Stomatal organization is anomocytic and sometimes subsidiary cells, smaller than neighboring epidermal cells, are evident. The mesophyll in some species of *Saxifraga* L. is undifferentiated, and in species where it is differentiated, the palisade segment may range from 1 to 7 cells deep. Hydathodes are of common occurrence. Petiolar vasculature is distinctive, especially in *Saxifraga* where one concentric bundle or one hemi-concentric bundle may occur. In other species of *Saxifraga*, there are three such bundles, each with its own endodermis. Some Saxifragaceae have the usual collateral bundles, but these may be scattered. The herbaceous Saxifragaceae resemble Columelliaceae in the presence of an anomocytic stomatal apparatus, apparently modified in some taxa; but the undifferentiated mesophyll in some species of *Saxifraga* and multilayered palisade tissues in others, are very different from the condition in *Columellia*. Petiolar vasculature in Saxifragaceae bears little resemblance to that in Columelliaceae.

Leaves in Grossulariaceae are dorsiventral and bear unicellular and

also glandular hairs. Pairs of small, circular guard cells are characteristic. The petiole is characterized by three separate vascular strands at the base which fuse distally to produce a single crescentiform strand all supported by sclerenchyma in the "pericyclic" region. The specialized, small circular guard cells vary from those in Columelliaceae but the abaxial sclerenchyma associated with the petiolar bundle also occurs in Columelliaceae. The proximally triple vascular strand differs from the condition in Columelliaceae.

All leaves in Escalloniaceae are dorsiventral. In *Escallonia*, foliar hairs are thick-walled and unicellular; in *Abrophyllum* Hook.f., hairs are glandular with unicellular heads; in some species of *Escallonia* hairs are glandular-shaggy with multiseriate stalks; in *Quintinia* A. DC. peltate hairs occur; and T-shaped hairs occur in *Argophyllum*. Stomatal organization is variable and pairs of nearly circular, small guard cells, resembling those in Grossulariaceae, occur in *Escallonia*, *Itea* L., and other genera; the stomatal apparatus in *Quintinia* is paracytic; and the stomatal apparatus in *Brexia* is characterized by a double front cavity. A 1-3-layered upper hypodermis occurs in species of *Argophyllum*, *Carpodetus*, *Escallonia*, and other genera. A single-layered palisade mesophyll is present in two genera. Three vascular bundles enter the base of the petiole in *Escallonia*, but in *E. macrantha* Wedd. (= *E. polifolia* Hook.) and *E. rubra* (Ruiz & Pavón) Pers., a single crescentiform petiolar bundle with accessory strands is present. Apparently there is no abaxial sclerenchyma present in *Escallonia*. *Brexia* appears unique, for besides the abaxial, crescentiform vascular strand in the petiole, there is also a small cylinder of xylem in the medullary region and two abaxial xylem cylinders. Certain similarities between Columelliaceae and Escalloniaceae occur: unicellular, thick-walled hairs; presence of a hypodermis; and a single petiolar vascular strand in at least two species of *Escallonia*. However, there are also marked differences and Escalloniaceae show glandular and multicellular hairs, grossulariaceous stomatal organization, and a triple vascular condition in petioles of most species of *Escallonia*.

Hydrangeaceous leaves are dorsiventral. Hairs are various with long, unicellular trichomes in *Jamesia*; tufted trichomes in *Broussaisia* Gaudich. and *Pileostegia* Hook. f. & Thoms.; and stellate, calcified, and unicellular types in *Deutzia* Thunb. Glandular leaf teeth occur in *Decumaria* L., *Deutzia*, and *Philadelphus*. A hypodermis occurs in *Broussaisia* and in species of *Hydrangea*, and the epidermis contains some horizontally divided cells in *Carpenteria* Torr. The stomatal organization is paracytic in species of *Dichroa* Lour. and *Hydrangea* L. and anomocytic in *Philadelphus*. Palisade mesophyll is uniseriate in *Deutzia* and *Philadelphus*. The petiolar vascular strand differs throughout the family: It is single and crescent-shaped in species of *Deutzia*, *Jamesia*, *Philadelphus*, *Hydrangea*, and *Pileostegia*; petioles of *Decumaria sinensis* Oliv., *Dichroa febrifuga* Lour., and *Hydrangea petiolaris* Sieb. & Zucc. are characterized by a main abaxial arc with several flat adaxial bundles between the ends.

Additional strands are present in other species, including medullary bundles. Although some foliar similarities exist between some taxa of Hydrangeaceae and Columelliaceae — unicellular hairs, glandular leaf teeth, hypodermis, anomocytic stomatal organization, and arcuate petiolar vascular supply — the differences are equally clear. Multicellular and tufted hairs, paracytic stomatal organization, and multistranded petiolar vascular supply occur in Hydrangeaceae.

The remaining plant families which have at one time or another been suggested as near relatives of Columelliaceae or *Columellia* — Scrophulariaceae, Ebenaceae, Loganiaceae, Oleaceae, Lythraceae, Vacciniaceae, Ericaceae, Gentianaceae, and Onagraceae — present a wide array of foliar anatomical features, some similar and others different from Columelliaceae. As should be apparent from the brief comparative summary above, no family presents a consistent foliar pattern which is similar enough in most respects to that in Columelliaceae to convince the critical botanist that leaf anatomy is a key to understanding the relationships of the family. To be sure, this is probably related to the lack of thorough anatomical investigation in those taxa reputedly related to Columelliaceae, but as the situation stands now, foliar anatomy is at its best equivocal in pointing the way to the relationships of Columelliaceae.

#### Evidence from nodal anatomy

According to Sinnott's (1914) survey of the nodal condition among seed plants, all members of the Tubiflorae, which include Scrophulariaceae and Gesneriaceae, are unilacunar. However, three or five gaps are typical for *Cyrtandra* J. R. & G. Forst. (Gesneriaceae). Onagraceae, Ericaceae, Ebenaceae, Oleaceae, Gentianaceae, Loganiaceae, and Rubiaceae, are also characterized by unilacunar nodes. In addition, some members of Gentianaceae are multilacunar and some Rubiaceae are trilacunar. Caprifoliaceae are generally tri- and sometimes pentalacunar. Cucurbitaceae are all trilacunar. Rosales, which include Saxifragaceae (treated in the broad Englerian sense by Sinnott), are said to be mostly trilacunar although five gaps occur in Brunelliaceae and in a few Saxifragaceae, Rosaceae, and Leguminosae. Platanaceae exhibit seven gaps.

Plant orders are remarkably constant with respect to their nodal conditions but Sinnott recognized that nodal anatomy is only one character, that nodal structure is not always invariable, and that further study will necessitate changes in his outline. In 1955, Marsden and Bailey presented their penetrating analysis of the node and interpretation of the primitive nodal condition. In contrast to Sinnott's hypothesis that the trilacunar condition is basic and primitive, Marsden and Bailey provided evidence to indicate that the unilacunar, two-trace condition is ancestral and they indicated possible means for deriving both the unilacunar, single-trace condition and the trilacunar, triple-trace condition directly from it. Furthermore, they hypothesized that the unilacunar node could give rise to the trilacunar node through amplification, much as Sinnott derived the multilacunar form from the trilacunar.

Takhtajan's (1964) scheme of nodal evolution is similar to that of Sinnott in that he accepted the primitiveness of the trilacunar node. However, the median lacuna has a double trace: "Thus, from all of these data one can conclude, it seems to me, that the node with three or more lacunae (FIG. 9) is the primary type of node in angiosperms. At present, it is impossible to determine more accurately the initial nodal type in angiosperms."

Because of the studies of Marsden and Bailey, it is apparent that a reassessment of the taxonomic value of nodal anatomy, as exemplified by Sinnott's treatment, is very much in order. The derivation of the unilacunar, one-trace condition in Columelliaceae, rather than the condition itself, is the key to taxonomic understanding. This is also true of the nodal configuration in all putative relatives. We cannot say that Columelliaceae is unrelated to saxifragaceous families because these are largely characterized by trilacunar nodes, nor can we assign the relationship of Columelliaceae to those families with unilacunar nodes, if we agree with Marsden and Bailey that, "Structures which appear to be similar at the nodal level may not be truly homologous, and conversely differences which seem outstanding at the nodal level may acquire a different significance where comprehensive developmental studies at successive levels of the stem and leaf are made."

#### Evidence from xylem anatomy<sup>5</sup>

A brief recapitulation of the salient features in the xylem anatomy of Columelliaceae is in order here: perforation plates scalariform; pore distribution exclusively solitary; intervacular pitting usually absent, except tending to alternate in regions of ligular overlap between superposed vessel elements; axial parenchyma vasicentric scanty; vascular rays exclusively uniseriate consisting solely of upright cells; spiral thickenings present in walls of vessel elements; and imperforate tracheary elements are tracheids.

Gesneriaceae all have simple perforations in vessel elements. However, vestigial bars were noted in perforation plates of *Solenophora calycosa* Donn. Smith. In all woods examined, pores are solitary, in radial multiples, and in clusters except in *Solenophora* sp. (Yw 22822) where no clusters were observed. Intervacular pitting is exclusively alternate, except in *Solenophora calycosa* where transitional pitting was also seen. Axial parenchyma distribution is various; however, it is paratracheal except for *Drymonia spectabilis* (H.B.K.) Mart., *Rhytidophyllum crenulatum* DC., and *Solenophora calycosa*, in which diffuse parenchyma occurs. In most species the vasicentric parenchyma is scanty; vasicentric parenchyma is abundant, however, in *Columnnea purpurata* Hanst., *Cyrtandra oenobar-*

<sup>5</sup>Anatomical data presented in this section are based on original observations in Gesneriaceae, Grossulariaceae, Hydrangeaceae, and Escalloniaceae. Microscope slides examined were from the Yale (Yw) and Smithsonian (USw) wood collections. Data from other families are from the literature. For convenience in making comparisons, families are considered as circumscribed in Metcalfe and Chalk (1950).

*bata* H. Mann, *C. spathacea* A. C. Smith, and *Gesneria* sp. (Yw 16832). In *Drymonia* sp. (Yw 17724), aliform and aliform-confluent parenchyma occurs. Vascular rays are absent in *Besleria* spp. (Yw 12217, 12225). In *Columnea purpurata* rays are 1 to 3 cells wide and in *Solenophora calycosa*, rays are mostly uni- and biseriate. In all other species investigated, rays are multiseriate. Rays are homocellular consisting solely of upright cells in *Drymonia spectabilis*, *Columnea purpurata*, *Rhytidophyllum crenulatum*, *R. tomentosum* (L.) Mart., and *Rhytidophyllum* sp. (Yw 20017). Heterocellular rays occur in *Cyrtandra oenobarbata*, *C. spathacea*, *Gesneria* sp. (Yw 16832), *Drymonia* sp. (Yw 17724), *Solenophora calycosa*, and *Solenophora* sp. There are no spiral thickenings in vessels of Gesneriaceae. Imperforate tracheary elements are various: septate elements occur in *Besleria* spp., *Gesneria* sp., *Drymonia spectabilis*, *Columnea purpurata*, *Rhytidophyllum crenulatum*, *R. tomentosum*, *Solenophora calycosa*, and *Solenophora* sp. Only *Cyrtandra* did not show septate imperforate tracheary elements. *Drymonia spectabilis* exhibits only fiber-tracheids and *Gesneria* sp., *Drymonia* sp., *Rhytidophyllum crenulatum*, and *Solenophora* sp. show only libriform wood fibers. All other species investigated show both fiber-tracheids and libriform wood fibers.

Except for the common occurrence of vasicentric scanty axial parenchyma in Gesneriaceae and Columelliaceae, the wood anatomy of these two families is very different. Perforation plates in Columelliaceae are scalariform; in Gesneriaceae they are simple. Pore distribution is strictly solitary in Columelliaceae; in Gesneriaceae it is solitary and in radial multiples and clusters in most of the species studied. Intervascular pitting is virtually absent in Columelliaceae because of the independent distribution of vessels; in Gesneriaceae it is alternate. All species of Columelliaceae have vascular rays; in Gesneriaceae, *Besleria* lacks vascular rays. Vascular rays are uniseriate in Columelliaceae; in Gesneriaceae all species have vascular rays more than one cell wide. Vascular rays contain only upright cells in Columelliaceae; in Gesneriaceae species may show both heterocellular rays and homocellular rays with upright cells. Spiral thickenings are present in the vessels of Columelliaceae; in Gesneriaceae, vessels lack spiral thickenings. In Columelliaceae all imperforate tracheary elements are tracheids; in Gesneriaceae both fiber-tracheids and libriform wood fibers occur, but no tracheids.

Grossulariaceae have scalariform perforations in vessel elements, but some simple perforations were also observed. Pores are solitary, in radial multiples, and in clusters. Growth rings are pronounced and the wood is ring porous. Intervascular pitting is transitional and scalariform. Axial parenchyma is absent. Vascular rays are multiseriate, broad, and heterocellular. Sheath cells are of common occurrence in the rays. Spiral thickenings are absent from vessel walls. Imperforate elements are septate tracheids and in *Ribes viscosissimum* Pursh, fiber-tracheids were also recorded.

The presence of scalariform perforations and tracheids seems to pro-

vide the only common anatomical features between Grossulariaceae and Columelliaceae. Solitary, radial multiple, and clustered pores; ring porosity; broad, heterocellular vascular rays; septate imperforate tracheary elements; and the absence of axial parenchyma in the wood of Grossulariaceae are rather distinct anatomical characteristics which differ from Columelliaceae.

Perforation plates in vessel elements of Hydrangeaceae are scalariform.<sup>6</sup> Pores are exclusively solitary in *Broussaisia arguta* Gaudich., *B. pellucida* Gaudich., *Fendlera rupicola* A. Gray, and *Philadelphus* sp. (Yw 11845). In *Deutzia vilmorinae* Lemoine & D. Bois, *Hydrangea panamensis* Standley, and *Philadelphus coronarius* L., pores are solitary and in radial multiples. *Hydrangea bretschnideri* Dipp. and *Dichroa febrifuga* show pores in solitary, radial multiple, and clustered dispositions. Intervascular pitting is generally absent in *Broussaisia arguta*, *B. pellucida*, and *Fendlera rupicola*. However, in the overlapping vessel ligules of *Broussaisia arguta*, scalariform pitting was seen, whereas in this position *Fendlera rupicola* shows a tendency to alternate intervacular pitting. In *Philadelphus coronarius*, intervacular pitting is transitional; in *Philadelphus* sp., pitting is alternate with some opposite. Pitting in vessel walls of *Deutzia vilmorinae*, *Hydrangea bretschnideri*, and *H. panamensis* is scalariform. Vessel walls in *Dichroa febrifuga* show both transitional and scalariform pitting. Axial xylem parenchyma is diffuse and vasicentric scanty in all species studied. No axial parenchyma was observed in *Fendlera rupicola* and *Hydrangea bretschnideri*. In all species studied, homocellular uniseriate rays were present in which cells are upright. These occur in conjunction with other heterocellular rays, two or more cells wide. Rays up to 8-cells wide occur in *Broussaisia pellucida*. *Deutzia vilmorinae*, *Fendlera rupicola*, and *Hydrangea bretschnideri* have only uni- and biseriate rays. Sheath cells are common in species with wide rays. In *Deutzia vilmorinae*, scalariformly perforated ray cells occur. Tenuous spiral thickenings occur in the cell walls of vessels and tracheids of *Fendlera rupicola*; in *Philadelphus coronarius* and *Philadelphus* sp., spirals occur in tracheids. Imperforate tracheary elements in *Fendlera rupicola*, *Hydrangea bretschnideri*, *Philadelphus coronarius*, and *Philadelphus* sp., are exclusively tracheids. In *Broussaisia arguta*, *B. pellucida*, and *Dichroa febrifuga*, both tracheids and fiber-tracheids appear. *Deutzia vilmorinae* and *Hydrangea panamensis* show only fiber-tracheids. Imperforate tracheary elements are septate in *Hydrangea panamensis* and *Dichroa febrifuga*.

There are several similarities between the woods of some species of Hydrangeaceae and Columelliaceae: scalariform perforation plates, exclusively solitary pores and concomitant absence of intervacular pitting, a tendency to alternate intervacular pitting, and tracheids. Axial xylem parenchyma is vasicentric scanty in Columelliaceae with some diffuse; in

<sup>6</sup> Metcalfe and Chalk (1950) report simple perforation plates in *Deutzia glabrata* Kom. and in some species of *Philadelphus*.

all Hydrangeaceae studied, where axial xylem parenchyma was present, it is vasicentric scanty and some strands were diffusely arranged. On the other hand, there are also pronounced anatomical differences between these families: Pores are exclusively solitary in Columelliaceae; in several species of Hydrangeaceae pores are in both solitary and other arrangements. Intervascular pitting tends toward alternate in Columelliaceae; in Hydrangeaceae scalariform and transitional intervacular pitting occur in several species. All species of Columelliaceae show axial parenchyma; several species of Hydrangeaceae lack this tissue. In Columelliaceae, vascular rays are all uniseriate and homocellular; all Hydrangeaceae have uniseriate rays plus rays which are two or more cells wide and heterocellular. Imperforate tracheary elements in Columelliaceae are tracheids; some species of Hydrangeaceae show both tracheids and fiber-tracheids, while other species have only fiber-tracheids.

Perforation plates in Escalloniaceae are exclusively scalariform except in *Brexia*, where plates are mostly simple, and in *Kania* Schlechter,<sup>7</sup> where they are exclusively simple. All Escalloniaceae have solitary pores; in *Escallonia floribunda* H.B.K., *E. jonkii* Phil., and *E. myrtilloides* L.f., pores are exclusively solitary. In *E. pulverulenta* (Ruiz & Pavón) Pers., *E. revoluta* (Ruiz & Pavón) Pers., *E. rubra* (Ruiz & Pavón) Pers., and *E. tortuosa* H.B.K., pores are also in radial multiples. Pores are solitary and in radial multiples in *Brexia madagascariensis* Thou. ex Ker-Gawl., *Itea* sp. (Yw 20142), *Quintinia acutifolia* T. Kirk, *Q. serrata* A. Cunn., and *Q. sieberi* A. DC. In *Quintinia*, however, multiples are rare but tangentially oriented groups of pores are conspicuous. Solitary, radial multiple, and clustered dispositions are seen in *Anopterus glandulosus* Labill., *Argophyllum ellipticum* Labill., and in all *Polyosma* species studied. Intervascular pitting is sparse in *Quintinia acutifolia* and *Q. serrata*; pitting in *Q. sieberi* is alternate with a tendency to opposite. In those species of *Escallonia* with exclusively solitary pore distribution, the widely overlapping vessel ligules provide areas of intervacular communication showing alternate intervacular pitting. Species of *Escallonia* with radial pore multiples show alternate intervacular pitting. Alternate intervacular pitting also occurs in *Anopterus macleayanus* F. Muell., *Argophyllum ellipticum*, *Brexia madagascariensis*, *Itea* sp., and in all *Polyosma* species studied except *P. integrifolia* Blume and *P. serrulata* Blume which have exclusively opposite pitting. In addition to alternate intervacular pitting, *Anopterus macleayanus* and *Escallonia floribunda* show transitional pitting. *Anopterus glandulosus* only has transitional intervacular pitting. In addition to alternate pitting, *Itea* sp. shows transitional and scalariform pitting. All species of *Polyosma* with alternate intervacular pitting also show opposite pitting. Escalloniaceae are characterized by apotracheal axial parenchyma and all species studied show either a diffuse and/or

<sup>7</sup> Erdtman and Metcalfe (1963) have assigned this genus to Myrtaceae on anatomical and palynological grounds. Their evidence is so strong, that *Kania* will not be considered further in this discussion.



diffuse-in-aggregates pattern. In *Escallonia revoluta*, *E. rubra*, all species of *Polyosma*, and *Quintinia sieberi*, both diffuse and diffuse-in-aggregates patterns occur. In *Anopterus glandulosus*, *Escallonia myrtilloides*, *E. tortuosa*, *Itea* sp., *Quintinia acutifolia*, and *Q. serrata*, only diffuse axial parenchyma was observed. Parenchyma in *Brexia madagascariensis* consists of multiseriate bands. Short uniseriate bands occur in *Escallonia floribunda*, in addition to the diffuse-in-aggregates pattern. Axial parenchyma is absent in *Argophyllum ellipticum*. All species of Escalloniaceae have some uniseriate rays, although none was observed in *Anopterus glandulosus* where rays are exclusively multiseriate. All species have some heterocellular rays except for *Brexia madagascariensis*. The following species has uni- and biseriate rays only: *Anopterus macleayanus*, *Brexia madagascariensis*, *Escallonia myrtilloides*, and *E. tortuosa*. All other species studied have both uniseriate rays and rays which are two or more cells wide. Vascular rays are exclusively heterocellular in *Anopterus glandulosus*, *A. macleayanus*, *Argophyllum ellipticum*, and *Escallonia floribunda*. Rays in *Brexia madagascariensis* are homocellular and cells are upright. In the following species, multiseriate and biseriate rays are heterocellular and uniseriate rays are homocellular containing only upright cells: *Escallonia jonkii*, *E. myrtilloides*, *E. pulverulenta*, *E. revoluta*, *E. rubra*, *E. tortuosa*, *Itea* sp., and all species of *Polyosma* and *Quintinia*. Species with wide multiseriate rays commonly exhibit sheath cells. Spiral thickenings occur in walls of vessels in *Escallonia floribunda*, *E. myrtilloides*, *E. rubra*, and *E. tortuosa*. In *E. myrtilloides* and *E. tortuosa*, spiral thickenings also occur in tracheid walls. Only tracheids occur in *Anopterus glandulosus*, *Escallonia floribunda*, *E. myrtilloides*, *E. revoluta*, *E. rubra*, *E. tortuosa*, *Polyosma cunninghamii* Benn., and *Quintinia*. Both tracheids and fiber-tracheids occur in *Anopterus macleayanus*, *Escallonia pulverulenta*, and *Itea* sp. *Argophyllum ellipticum*, *Brexia madagascariensis*, *Escallonia jonkii*, *Polyosma cambodiana* Gagn. (?), *P. ilicifolia* Blume, *P. integrifolia*, *P. mutabilis* Blume, and *P. serrulata*, exhibit only fiber-tracheids. Septate fiber-tracheids appear in *Argophyllum ellipticum*.

The xylem anatomical similarities between species of Escalloniaceae and Columelliaceae are striking: exclusively scalariform perforation plates (except in *Brexia*), exclusively solitary pore distribution (in some species of *Escallonia* and in *Polyosma cunninghamii*), spiral thickenings in vessels (in some species of *Escallonia*), and exclusively tracheids (in *Anopterus glandulosus*, in some species of *Escallonia*, *Polyosma cunninghamii*, and *Quintinia*). The only major anatomical differences between these two families are the presence of vascular rays which are two or more cells wide and exclusively apotracheal axial parenchyma in all Escalloniaceae. Among the species studied, the xylem anatomy of *Escallonia myrtilloides* can hardly be distinguished from that of Columelliaceae, except for the biseriate condition of some of the rays and exclusively diffuse axial parenchyma in the former (cf. FIGS. 22 and 23, 24 and 25, 26 and 27).

Among the remaining families which have been suggested as close relatives of Columelliaceae — Ebenaceae, Styracaceae, Gentianaceae, Logan-

iaceae, Caprifoliaceae, Rubiaceae, Onagraceae, Oleaceae, Vacciniaceae, and Scrophulariaceae — xylem anatomy provides serious bases for comparison only with Styracaceae, Caprifoliaceae, and Vacciniaceae. Styracaceae typically show scalariform perforation plates and uniseriate, homocellular vascular rays in some species; some Caprifoliaceae have scalariform and simple perforation plates, spiral thickenings in vessels, and imperforate tracheary elements with distinctly bordered pits; and most Vacciniaceae have scalariform or scalariform and simple perforations and imperforate tracheary elements with distinctly bordered pits. Ebenaceae, Loganiaceae, Rubiaceae, Onagraceae, Oleaceae, and Scrophulariaceae, are characterized by simple perforations. In addition, Gentianaceae-Gentianoideae universally possess internal phloem and medullary vascular bundles; Loganiaceae-Loganioideae are characterized by included phloem; and Onagraceae have internal phloem in the axis and a few genera show included phloem. These dispositions of phloem are very specialized and are ordinarily indicative of close relationship within specific taxa, sometimes on an ordinal basis (e.g., internal phloem in families of Myrtales).

#### CONCLUSION

In reviewing the foregoing presentations of evidence and discussions, it is clearly impossible to assemble an array of data from each form of evidence presented — gross morphology, floral anatomy, foliar anatomy, nodal anatomy, and xylem anatomy — which would affirm unequivocally the relationships of Columelliaceae with any one of the several families to which it has been allied. The similarities in gross morphology of flowers and fruits among many families of various alliances probably indicates parallel evolution rather than close genetic relationship. The evolutionary development which has culminated in *Columellia* has proceeded in such a manner that the complex of its characteristics is different from any known taxon today. What baffles us now baffled our predecessors and it is time to admit once and for all that Columelliaceae is a unique plant family, probably with no really close living relatives. The clearest line of evidence for the possible relationships of Columelliaceae is provided by xylem anatomy and it appears not too far from reality to assert that this family belongs in the great saxifragaceous assemblage with the Escalloniaceae, Hydrangeaceae, and Grossulariaceae. Data from gross morphology, floral anatomy, palynology, etc., at least do not contradict this probability. Perhaps its nearest relatives are in the Escalloniaceae. If there was a common saxifragaceous ancestor, phylogenetic departure must have occurred long ago, for transitional forms seem to have been lost in the development of the modern plants of which this taxon is composed. Evidence from xylem anatomy seems equally persuasive in negating an alliance with any other family or group of families. Unfortunately, data from cytotaxonomy, embryology, and biochemistry, which might be helpful in resolving our somewhat equivocal stand, are not available for *Columellia*.

## ACKNOWLEDGMENTS

This study has been carried out under the sponsorship of the Yale School of Forestry, the Smithsonian Institution, the Arnold Arboretum of Harvard University, and the University of Maryland. We are grateful to administrators of these institutions for the privilege of using their facilities. For their encouragement, suggestions, and critical advice, we wish to acknowledge warmly Dr. Sherwin Carlquist, Dr. Robert F. Thorne, Dr. Arthur Cronquist, and Dr. Hugh Iltis. The administrators of various herbaria have been cooperative in allowing us to see specimens *in situ*, to borrow specimens for study, and to use bits of stems, leaves, and flowers for microscopic observations: Royal Botanic Gardens, Kew; Yale School of Forestry, New Haven; Herbario San Marcos, Museo de Historia Natural, Lima; Arnold Arboretum and Gray Herbarium, Harvard University, Cambridge; Field Museum of Natural History, Chicago; U.S. National Herbarium, Smithsonian Institution, Washington; and New York Botanical Garden, Bronx. Microscope slides and woods for sectioning of *Columellia* and other taxa were made available from the Record Memorial Collection of the Yale School of Forestry and from the collections of the Division of Plant Anatomy, Department of Botany, Smithsonian Institution. We appreciate the generous cooperation of botanists in these institutions. Dr. Oscar Továr of the Herbario San Marcos, Lima, provided the only fluid-preserved anatomical specimens of *Columellia* available to us and we are especially thankful for his efforts in our behalf. Dr. John J. Wurdack, Smithsonian Institution, kept our needs in mind during a collecting trip to Peru and provided us with a fine wood sample of *C. oblonga* ssp. *oblonga*. Mr. James Teeri, of the University of New Hampshire, and Miss Carolyn Bensel, who is working on the floral anatomy of the Saxifragaceae, *sensu lato*, in Dr. Barbara Palser's laboratory at Rutgers University, were most kind to share their observations with us in advance of publication. We also extend our thanks to Mr. Austin Griffiths, Jr., of the Los Angeles State and County Arboretum for preserved flowers of *Escallonia*; to Miss Brenda Gee, of the University of Auckland, for preserved flowers of *Carpodetus*; and Dr. Judy Morgan for help with the sectioning and examination of floral material.

## LITERATURE CITED

- AGABABYAN, V. SH. 1964. Ėvolutsiya pyl'tsy v poryadkakh Cunoniales i Saxifragales v svyazi s nekotorymi voprosami ikh sistematiki: filogenii. Izv. Akad. Nauk Armyanskoï SSR, Biol. Nauki 17(1): 59-72; tab. I-III.
- AGARDH, J. G. 1858. Theoria systematis plantarum. xcvi + 404 pp. pls. 28. C. W. K. Gleerup. Lundae.
- ARNOTT, H. J. 1959. Leaf clearings. Turtox News 37: 192-194.
- BAILLON, H. 1888. Gesnériacées. Histoire des plantes. 10: 59-110. Librairie Hachette. Paris.
- BARTLING, F. T. 1830. Ordines naturales plantarum. Dieterichianus. Gottingae.

- BENTHAM, G., & J. D. HOOKER. 1876. *Columelliaceae*. *Genera plantarum*. 2: 989. L. Reeve & Co. London.
- BHATTACHARJYA, S. S. 1954. Ein Beitrag zur Morphologie des Androeceums von *Benincasa hispida* (Thunb.) Cogn. *Ber. Deutsch. Bot. Ges.* 67: 22-25.
- BRIZICKY, G. K. 1961. A synopsis of the genus *Columellia* (Columelliaceae). *Jour. Arnold Arb.* 42: 363-372.
- CANDOLLE, A. P. DE. 1839. *Columelliaceae*. *Prodromus systematis naturalis regni vegetabilis*. 7: 549. Truettel & Würtz. Paris.
- CHAKRAVARTY, H. L. 1958. Morphology of the staminate flowers in the Cucurbitaceae with special reference to the evolution of the stamen. *Lloydia* 21: 49-87.
- CLARKE, B. 1858. On the anthers of *Columelliaceae* and *Cucurbitaceae*. *Ann. Mag. Nat. Hist. London*. III. 1: 109-113; *pl. VI*.
- COMMITTEE ON NOMENCLATURE, INTERNATIONAL ASSOCIATION OF WOOD ANATOMISTS. 1957. International glossary of terms used in wood anatomy. *Trop. Woods* 107: 1-36.
- CRONQUIST, A. 1968. The evolution and classification of flowering plants. x + 396 pp. Houghton Mifflin. Boston.
- DON, D. 1828. Descriptions of *Columellia*, *Tovaria*, and *Francoa*; with remarks on their affinities. *Edinburgh New Philos. Jour.* 1828-1829: 46-53.
- DON, G. 1838. *Columellieae*. A general history of the dichlamydeous plants. 4: 57, 58. J. G. & F. Rivington. London.
- ENDLICHER, S. 1839. *Columelliaceae*. *Genera plantarum*. 1839: 745. Fr. Beck. Vindobonae.
- . 1841. *Columelliaceae*. *Enchiridion botanicum*. 366 pp. Guil. Engelmann. Lipsiae-Viennae.
- ENGLER, A. 1892. Syllabus der Vorlesungen über specielle und medicinisch-pharmaceutische Botanik. xxiii + 184 pp. Gebrüder Borntraeger. Berlin.
- . 1928. *Saxifragaceae*. *Nat. Pflanzenfam.* ed. 2. 18a: 74-226.
- ERDTMAN, G. 1952. Pollen morphology and plant taxonomy. *Angiosperms*. xii + 539 pp.; *frontis*. Almquist & Wicksell. Stockholm.
- & C. R. Metcalfe. 1963. Affinities of certain *genera incertae sedis* suggested by pollen morphology and vegetative anatomy. *Kew Bull.* 17: 249-256; *pl. 2*.
- ESAU, K. 1965. *Plant anatomy*, ed. 2. xx + 767 pp. John Wiley & Sons. New York.
- EYDE, R. H. 1966. Systematic anatomy of the flower and fruit of *Corokia*. *Am. Jour. Bot.* 53: 833-847.
- FAHN, A. 1967. *Plant anatomy* (Transl. by SYBIL BROIDO-ALTMAN). vii + 534 pp. Pergamon Press. New York.
- FELDHOFEN, E. 1933. Beiträge zur physiologischen Anatomie der nuptialen Nektarien aus den Reihen der Dikotylen. *Beih. Bot. Centralbl.* 50: 459-634; *Taf. II-XXXI*.
- FRITSCH, K. 1893, 1894. *Gesneriaceae*. *Nat. Pflanzenfam.* IV. 3b: 133-185 (133-144, 1893; 145-185, 1894).
- . 1894. *Columelliaceae*. *Nat. Pflanzenfam.* IV. 3b: 186-188.
- GELIUS, L. 1967. Studien zur Entwicklungsgeschichte an Blüten der Saxifragales sensu lato mit besonderer Berücksichtigung des Androeceums. *Bot. Jahrb.* 87: 253-303.
- GRISEBACH, A. H. R. 1839. *Genera et species gentianearum*. viii + 364 pp. J. G. Cottae. Stuttgartiae et Tubingae.

- HALLIER, H. 1901. Über die Verwandtschaftsverhältnisse der Tubifloren und Ebenalen. *Abh. Naturw. Ver. Hamburg* 16(2): 1-112.
- . 1903. Ueber die Abgrenzung und Verwandtschaft der einzelnen Sippen bei den Scrophularineen. *Bull. Herb. Boiss.* II. 3: 181-207.
- . 1908. Über *Juliania*, eine Terebinthaceen-Gattung mit Cupula, und die wahren Stammeltern der Kätzchenblütler. 210 pp. C. Heinrich. Dresden.
- . 1910. Ueber Phanerogamen von unsicherer oder unrichtiger Stellung. *Meded. Rijks Herb. Leiden* 1: 1-41.
- HERZOG, T. 1915. Die von Dr. Th. Herzog auf seiner zweiten Reise durch Bolivien in den Jahren 1910 und 1911 gesammelten Pflanzen. II Teil. *Meded. Rijks Herb. Leiden* 27: 1-90; *pl.* 1.
- HOOKE, J. D. 1873. "Editor's note." *In*: E. LE MAOUT & J. DECAISNE, A general system of botany. (Transl. by MRS. HOOKE; edited by J. D. HOOKE.) xii + 1066 pp. Longmans, Green, and Co. London. [Editor's note, 594].
- . 1875. *Columellia oblonga*. *Curtis's Bot. Mag.* 101: *tab.* 6183. L. Reeve & Co. London.
- HUTCHINSON, J. 1959. The families of flowering plants. ed. 2. 1: xi + 510 pp. Clarendon Press. Oxford.
- . 1967. The genera of flowering plants. 2: 659 pp. Clarendon Press. Oxford.
- JUSSIEU, A. DE. 1848. Taxonomie. *In*: A. C. V. D. D'ORBIGNY, Dictionnaire universel d'histoire naturelle. 12: 368-434. Renard, Martinet. Paris.
- JUSSIEU, A. L. [DE]. 1801. Responsa ad dubia clar. *In*: H. RUIZ & J. PAVÓN. Suplemento á la Quinologia. Imprenta de la Viuda e Hijo de Marin. Madrid. [*Columellia*, 147].
- KOMAR, G. A. 1967. O prirode nizhnei zavyazi Kryzhovnikykh (Grossulariaceae). *Bot. Zhur.* 52: 1611-1629.
- KRIBS, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* 96: 547-556.
- KUNTH, C. S. 1818. *Columellia*. Ruiz et Pav. *In*: A. VON HUMBOLDT, A. BONPLAND, & C. S. KUNTH, Nova genera et species plantarum. Quarto ed. 2: 388-389.
- LINDLEY, J. 1853. The vegetable kingdom. ed. 3. lxxviii + 908 pp. Bradbury & Evans. London.
- MARSDEN, M. P. F., & I. W. BAILEY. 1955. A fourth type of nodal anatomy in dicotyledons, illustrated by *Clerodendron trichotomum* Thunb. *Jour. Arnold Arb.* 36: 1-50.
- MCLEAN, D. M. 1947. Stamen morphology in flowers of the muskmelon. *Jour. Agric. Res.* 74: 49-54.
- MEISNER, C. F. 1836-1843. Plantarum vascularium genera. Pars 2. Commentarius. 401 pp. Libraria Weidmannia. Lipsiae. [*Columelliaceae*, 164, 165, 1840].
- MELCHIOR, H. 1964. *Columelliaceae*. *In*: A. ENGLER'S Syllabus der Pflanzenfamilien. ed. 12. 2: 464. Gebrüder Borntraeger. Berlin.
- METCALFE, C. R., & L. CHALK. 1950. Anatomy of the dicotyledons. 1: lxxiv, 1-724; 2: 725-1500. Clarendon Press. Oxford.
- MILLER, W. L. 1929. Staminate flower of *Echinocystis lobata*. *Bot. Gaz.* 88: 262-284.
- MORF, E. 1950. Vergleichend-morphologische Untersuchungen am Gynoeceum der Saxifragaceen. *Ber. Schweiz. Bot. Gesell.* 60: 516-590.

- PALMATIER, E. A. 1943. Some studies on the floral anatomy and morphology of the Saxifragaceae. Ph.D. Thesis, Cornell Univ., Ithaca. [Unpublished.]
- PHILIPSON, W. R. 1967. *Griselinia* Forst. fil. — anomaly or link. *N. Z. Jour. Bot.* 5: 134–165.
- PULLE, A. A. 1952. Compendium van de terminologie, nomenclatuur en systematiek der zaadplanten. 3de Druk. ix + 376 pp. A. Oosthoek's Uitgevers-Maatschappij. Utrecht.
- QUANG, L. T. 1963. Floral anatomy of the Cucurbitaceae. Ph.D. Thesis, Washington Univ., St. Louis. [Unpublished] [Diss. Abs. 26(2): 645–655. 1965].
- RAO, V. S., S. RAMARETHINAM, & L. IYER. 1964. The vascular anatomy of the flowers of Rubiaceae with special reference to the ovary. *Jour. Univ. Bombay, B.* 32(3 & 5): 163–231.
- REICHENBACH, H. G. L. 1828. *Conspectus regni vegetabilis per gradus naturales evoluti. Pars prima.* xiv + 294 pp. Carolus Cnobloch. Lipsiae.
- . 1837. *Handbuch des natürlichen Pflanzensystems.* x + 346 pp. Arnoldischen Buchhandlung. Dresden & Leipzig.
- RUIZ, H., & J. PAVÓN. 1794. *Florae peruviana, et chilensis prodromus.* xxii + 153 pp. *pls.* 37. Imprenta de Sancha. Madrid. [*Columellia*, 3, *pl.* 1].
- SCHLECHTER, R. 1920. Die Columelliaceae. *Notizbl. Bot. Gart. Mus. Berlin* 7: 352–358.
- SCHNIZLEIN, A. 1843–1870. *Iconographia familiarum naturalium regni vegetabilis.* 2: *pl.* 159\*\*\*. 1849. Max Cohen & Sohn. Bonn.
- SINNOTT, E. W. 1914. Investigations on the phylogeny of the angiosperms I. The anatomy of the node as an aid in the classification of angiosperms. *Am. Jour. Bot.* 1: 303–322.
- SOLEREDER, H. 1899. *Systematische Anatomie der Dicotyledonen.* xii + 984 pp. Ferdinand Enke. Stuttgart.
- SPRENGEL, C. 1830. *Caroli Linnaei, Genera plantarum.* ed. 9. 1: 870 pp. Dieterichianus. Gottingae. [*Columellia*, 25].
- STERN, W. L. 1967. Index xylariorum. *Reg. Veg.* 49: 1–36.
- & K. L. CHAMBERS. 1960. The citation of wood specimens and herbarium vouchers in anatomical research. *Taxon* 9: 7–13.
- TAKHTAJAN, A. 1959. *Die Evolution der Angiospermen* (Transl. by W. Höppner). viii + 344 pp. Gustav Fischer. Jena.
- . 1964. *Fundamentals of the evolutionary morphology of angiosperms.* 236 pp. "Nauka." Moscow and Leningrad. [In Russian].
- . 1966. *Systema et phylogenia magnoliophytorum.* 610 pp. "Nauka." Moscow and Leningrad. [In Russian].
- TEERI, J. A. 1968. Floral anatomy of *Kohleria*. (In press.)
- THORNE, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* 6: 57–66.
- TIEGHEM, P. VAN. 1903. Sur les Columelliacées. *Bull. Mus. Hist. Nat. Paris* 9: 233–239.
- WARBURG, O. 1922. *Die Pflanzenwelt.* 3: xii + 551 pp. *pls.* 1–28b. Bibliographisches Institut. Leipzig.
- WETTSTEIN, R. 1935. *Handbuch der systematischen Botanik.* ed. 4. x + 1152 pp. Franz Deuticke. Leipzig & Wien.
- WILLIS, J. C. 1966. *A dictionary of the flowering plants and ferns.* ed. 7. (Revised by H. K. AIRY SHAW). University Press. Cambridge.

WYLIE, R. B. 1952. The bundle sheath extension in leaves of dicotyledons.  
Am. Jour. Bot. 39: 645-651.

UNIVERSITY OF MARYLAND  
DEPARTMENT OF BOTANY  
COLLEGE PARK, MARYLAND 20740

HARVARD UNIVERSITY  
ARNOLD ARBORETUM  
CAMBRIDGE, MASSACHUSETTS 02138

SMITHSONIAN INSTITUTION  
DIVISION OF PLANT ANATOMY  
WASHINGTON, D.C. 20560

## NOTES ON THE DISTRIBUTION AND HABITAT OF COLUMELLIA

GEORGE K. BRIZICKY AND WILLIAM L. STERN

IN THE COURSE of an investigation on the taxonomic position of Columelliaceae, the authors had the opportunity to examine additional herbarium material of *Columellia* which was unavailable to Brizicky when he compiled his "Synopsis" of the genus (Jour. Arnold Arb. 42: 363-372, 1961). This material documents range extensions for the genus and for three of the species beyond those indicated in the "Synopsis." The authors believe that the publication of these extensions, and of additional collections not reported heretofore, will be of some interest to Neotropical botanists.

The range of *Columellia* Ruiz & Pavón, as it is known at present (FIG. 1), extends from southwestern Colombia southward to Ecuador, Peru (as far south as the departments of Cuzco, Urubamba, and Apurimac), and to the "yungas" of western Bolivia. Extensions of the ranges of species and additional collections are cited below.

***Columellia oblonga* Ruiz & Pavón.**

DISTRIBUTION: southern Colombia, Ecuador, Peru, and western Bolivia.

***Columellia oblonga* subsp. *oblonga*.**

Peru. AMAZONAS: prov. Chachapoyas, middle eastern Calla-Calla slopes, near kms. 415-418 of Leimebamba-Balsas road, elev. 2900-3150 m., *J. Wurdack* 1732 (US, A), Aug. 20, 1962. HUANCAVELICA: prov. Tayacaja, Ampurco, entre Salcambamba y Surcubamba, bosque perennifolio, alt. 3000 m., *O. Továr* 3785 (US), Apr. 19, 1962; alrededores de Huachocolpa, Valle del Mantaro, monte perennifolio, suelo arcilloso, nombre vulgar "yurac-chachas," alt. 2800-2900 m., *O. Továr* 4033 (USM), Apr. 16, 1963.

Some leaves in *Wurdack* 1732 are almost entire, approaching subspecies *sericea* in this character. This is not surprising, since the occurrence of specimens transitional between subspecies *oblonga* and subspecies *sericea* in that geographical area had already been reported in the "Synopsis."

***Columellia oblonga* subsp. *sericea* (H.B.K.) Brizicky.**

Colombia. NARIÑO: Cordillera Occidental, upper east slope of Volcán Gualcalá, 18 km. east of Piedranca, páramo on steep slope, vegetation chiefly grass and *Espeletia*, alt. 3500-3600 m., *F. R. Fosberg* 21175 (US), Oct. 5, 1943.

This collection by Fosberg is the first documented report of the species and the subspecies from Colombia. Pubescence on the lower side of leaves is less dense and the hairs are shorter than is typical for this subspecies.

Ecuador. IMBABURA: Cordillera Occidental, along trail to Piñan, slope of Volcán de Cotacachi, common near edge of páramo, alt. 10,400 ft., *W. B. Drew*